

UNIVERSITÉ DU QUÉBEC À MONTREAL

ENCLAVES FORESTIÈRES DÉCIDUES EN MATRICE AGRICOLE
ET
ACTIVITÉ REPRODUCTRICE D'UNE ESPÈCE AVIAIRE SENSIBLE AUX CONDITIONS
D'INTÉRIEUR DE FORÊT

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AVANT-PROPOS

Ce mémoire rassemble les résultats de mes travaux de maîtrise en biologie. Il comporte deux chapitres rédigés sous forme d'articles scientifiques en anglais qui sont compris entre une introduction générale et une conclusion générale rédigées en français. À titre de candidat à la maîtrise, j'ai procédé à l'élaboration du projet de recherche, à la récolte des données, à l'analyse des résultats et à la rédaction des articles à titre de premier auteur. Ces deux articles seront soumis à des revues scientifiques arbitrées : 1) Reproductive activity of Ovenbirds in a fragmented agricultural landscape in Southern Québec, et 2) Nesting success and population dynamics of Ovenbirds in a fragmented agricultural landscape: influence of local and landscape scale factors. Mon directeur de recherche, Pierre Drapeau, en est le coauteur.

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RÉSUMÉ

Plusieurs analyses des données démographiques des populations aviaires nord-américaines illustrent une importante fluctuation de l'abondance de certaines espèces au cours des dernières décennies. Soutenus par plusieurs années de recherche, les scientifiques attribuent ces fluctuations, entre autres causes, à la destruction et la fragmentation des habitats. Celles-ci engendrent trois facteurs inter-dépendants : la perte nette d'habitat, l'isolement des habitats résiduels et l'effet de bordure accru chez ces habitats. Le présent projet vise à mettre à jour les effets potentiels de la fragmentation forestière dans la plaine agricole du Saint-Laurent sur l'activité reproductrice d'une population de Paruline couronnée (*Seiurus aurocapillus*), une espèce reconnue sensible à la fragmentation du couvert forestier.

Ce mémoire contient deux chapitres. Le premier traite de la réponse démographique de la Paruline couronnée (densité, appariement, succès reproducteur à l'échelle des territoires contenant des couples nicheurs) en fonction du degré de morcellement du paysage dans le but de cibler les étapes du cycle reproducteur les plus affectées par la fragmentation d'un paysage forestier. Le deuxième chapitre examine à partir du suivi direct de nids, d'une part, les principales causes d'échecs à la nidification et discute, d'autre part, de la viabilité des populations locales de Paruline couronnée établies dans différents contextes de fragmentation.

En 2004 et 2005, 225 territoires de Paruline couronnée ont été recensés par la méthode des plans quadrillés (spot mapping) à l'intérieur de bois résiduels enclavés dans une matrice agricole (16 sites) et sur des sites témoins à l'intérieur d'une forêt continue (Mont Saint-Hilaire, Québec, Canada) (4 sites). Seuls des peuplements de forêts décidues et matures ont été sélectionnés, c'est-à-dire des peuplements de classe d'âge de 70 ans et plus dont la hauteur et la densité sont respectivement supérieurs à 17 mètres et 60%. Deux types de forêts résiduelles ont été échantillonnés : 1) des forêts connectées et 2) des forêts isolées.

Les résultats montrent que la densité et le succès d'appariement de la Paruline couronnée dans cette région ne sont pas affectés par le type d'habitat forestier. Cependant, la distance à une forêt continue (> 1000 ha de forêt profonde) a une influence négative sur la densité des mâles dans les forêts connectées sans toutefois en affecter le succès d'appariement. La proportion de territoires ayant mené au moins un jeune à l'envol n'a pas été affectée par la distance à une forêt continue mais a été significativement inférieure dans les forêts connectées et les forêts isolées que dans la forêt continue. Malgré un succès d'appariement élevé, le faible succès de reproduction à l'intérieur des forêts fragmentées indique que l'activité reproductrice dans ce système est fortement affectée à l'étape de l'incubation et du nourrissage des jeunes (chapitre 1). Cette situation est principalement provoquée par des niveaux élevés de prédation et de parasitisme par le Vacher à tête brune dans le paysage fragmenté (chapitre 2). Le rendement des habitats morcelés en termes de production de juvéniles est trop faible pour assurer le maintien de ces populations locales.

Cette étude suggère que sans le recrutement d'adultes en provenance des populations sources environnantes, les populations locales situées dans les fragments de forêts résiduelles sont susceptibles d'être non-viables à long terme. La faible variabilité inter-annuelle dans nos résultats, tant en forêt continue que dans les forêts fragmentées, suggère que les massifs de forêts continues, tels que le Mont Saint-Hilaire, jouent un rôle important en soutenant les populations locales d'oiseaux forestiers qui occupent les bois de petite et de grande taille de la vallée du Saint-Laurent.

Mots clés : *Seiurus aurocapillus*, fragmentation, appariement, succès de la reproduction, prédation, parasitisme.

INTRODUCTION GÉNÉRALE

1.1 Problématique

Les études des populations aviaires nord-américaines illustrent une importante fluctuation de l'abondance de plusieurs espèces au cours des dernières décennies. Alors que certaines populations augmentent ou se maintiennent, d'autres sont en forte diminution (Galli et al., 1976; Whitcomb, 1977; Lynch et Whitcomb, 1978; Whitcomb et al., 1981; Ambuel et Temple, 1983; Askins et al., 1990; Johnston et Hagan III, 1992; Peterjohn et al., 1997; Holmes et Sherry, 2001). Plusieurs facteurs ont été invoqués pour expliquer ces fluctuations.

Parmi les explications proposées, on compte certains phénomènes stochastiques tels les fluctuations climatiques et la variation de l'abondance des ressources (Holmes et al., 1986; Holmes et Sherry, 1988; Blake et al., 1992; Sauer et Droege, 1992), mais également des facteurs persistants dus aux activités humaines. Parmi ceux-ci figurent la perte et la fragmentation d'habitats aux aires d'hivernage et de reproduction (Hall, 1984; Johnston et Winings, 1987; Wilcove, 1985; Wilcove et al., 1986; Robbins et al., 1989b; Sauer et Droege, 1992; Tilman et al., 1994). Compte tenu de leur caractère cumulatif et de l'importance de leur contribution à l'endroit des fluctuations des populations aviaires nord-américaines, la perte et la fragmentation d'habitats ont considérablement retenu l'attention des scientifiques au cours des dernières décennies (Robbins, 1979; Whitcomb et al., 1981; Wilcove et Robinson, 1990; Andrén, 1994; Simberloff, 1994; Donovan et al., 1995; Kneeshaw, 1995; Fahrig, 1997; Villard et al., 1999; Burke et Nol, 2000; Bayne et Hobson, 2001; Lindenmayer et al., 2002).

1.2 Fragmentation des habitats

La fragmentation des habitats représente l'un des principaux phénomènes expliquant l'extinction locale, l'extirpation et la diminution de l'abondance affectant aujourd'hui plusieurs

espèces (Groombridge, 1992; Tilman et al., 1994). Concrètement, la fragmentation d'un habitat engendre trois facteurs interdépendants : la perte nette d'habitats, la réduction de la taille des habitats rémanents et l'augmentation de leur degré d'isolement (Bennett, 1999). Une perte nette d'habitats implique d'abord la disparition d'une certaine quantité d'habitats naturels à l'échelle régionale et se traduit par une diminution proportionnelle de l'abondance des populations habitant ces milieux. La réduction de la superficie occupée par l'habitat naturel est accompagnée de l'expansion d'un autre type de milieu généralement de nature anthropique. La présence de ce dernier, souvent hostile aux déplacements de certaines espèces mais bénéfique pour d'autres, influence la dynamique des populations locales établies dans les habitats résiduels. La réduction de la taille des habitats résiduels entraîne une augmentation des effets de lisière ainsi que l'accroissement de la distance entre les habitats qui résulte en la hausse du degré d'isolement (Bennett, 1999). Ces effets qui sont concomittants aux évènements de perte nette d'habitats en amplifient les conséquences négatives sur les populations animales, notamment en milieux forestiers (Andrén, 1994; Fahrig, 1997). D'une part, ces facteurs entraînent la diminution du taux de recolonisation des parcelles non occupées, et d'autre part, ils entravent l'activité reproductrice des espèces qui nichent dans les habitats fragmentés conduisant ainsi à des populations locales réduites plus vulnérables à l'extinction (Fahrig et Merriam, 1994).

La fragmentation de l'habitat est un phénomène pouvant engendrer une modification dans la dynamique des populations de plusieurs espèces. Quels en sont les impacts sur les populations aviaires forestières ? Sous quels paramètres pouvons-nous la quantifier ? Les forêts fragmentées de la plaine agricole du sud du Québec constituent-elles des habitats permettant l'accomplissement des cycles vitaux nécessaire au maintien de la diversité biologique ? Les populations aviaires forestières de la plaine agricole du Saint-Laurent sont-elles à risque ?

1.3 Importance de l'étude

Nous savons que la perte nette en habitats forestiers constitue l'un des principaux éléments pouvant expliquer la diminution des effectifs d'oiseaux migrateurs forestiers (Fahrig, 1997; Trzcinski et al., 1999). Cependant, bien que non-négligeable, l'importance des différents aspects associés à la fragmentation combinés à la perte nette d'habitats demeure méconnue (Villard et al., 1999). De ces aspects, on compte l'abondance, la taille et l'isolement des parcelles résiduelles. Bien que ces éléments soient inter-dépendants, il demeure important d'en connaître les effets respectifs sur les populations aviaires.

Plusieurs travaux ont abordé le sujet en examinant les effets de la fragmentation de l'habitat sur l'abondance des populations aviaires forestières (Villard et al., 1993; Villard et al., 1999; Holmes et Sherry, 2001; Donovan et Flather, 2002). L'abondance d'une espèce dans un habitat donné n'est cependant pas indicatrice de sa capacité à se reproduire efficacement dans cet habitat de manière à assurer un recrutement suffisant au maintien de la population locale. Bien que les variations d'abondance constituent une information importante quant à la dynamique des populations, il est possible que l'impact sur la reproduction soit différent. Les données quantitatives concernant les activités reproductrices sont donc essentielles à la détection de l'«effet puit» sous-jacent à la dynamique «source-puit» qui caractérise les populations subdivisées par la fragmentation des habitats (Pulliam et al., 1988).

Ces dernières années, une analyse de l'état des connaissances sur (1) la fragmentation des forêts du sud du Québec au moyen de divers outils cartographiques (Bélanger et Grenier, 1998; Duchesne et al., 1998; Service canadien de la faune, 1998a; Service canadien de la faune, 1998b) ainsi que (2) sur la distribution des populations d'oiseaux dans les environnements fragmentés du Sud du Québec (Freemark et al., 1991; Langevin et Bélanger, 1994) indiquent que l'abondance des populations d'oiseaux reconnues comme étant sensibles à la fragmentation des forêts feuillues est plus faible dans les forêts de paysages très fortement fragmentés (< 20% de forêt résiduelle) que dans les forêts de paysages qui le sont

de façon modérée (35–50% du territoire en forêts). Toutefois, ce résultat ne permet pas de connaître le statut de nidification de ces espèces dans les forêts fragmentées. Un individu peut effectivement être présent dans un boisé durant la période de nidification et défendre un territoire sans toutefois pouvoir s'y reproduire. Cette information est pourtant cruciale dans la détermination de la viabilité à long terme des populations biologiques. Ainsi, bien que l'on dispose de connaissances concernant le degré de morcellement des bois du Sud du Québec et leur utilisation par l'avifaune (Carignan, 2006), la qualité de ces milieux en tant qu'habitats de reproduction demeure méconnue.

À l'aide de données relatives à l'abondance, au succès d'appariement et au succès de reproduction recueillies auprès d'une population de Paruline couronnée (*Seiurus aurocapillus*), une espèce migratrice néotropicale sensible aux conditions d'intérieur de forêt, nous avons été en mesure d'évaluer la qualité des habitats forestiers résiduels de la vallée du Saint-Laurent.

1.4 Objectifs

La présente étude vise la bonification des connaissances concernant les effets de la fragmentation forestière causée par l'agriculture sur la démographie d'une espèce aviaire sensible aux conditions d'intérieur de forêt. Les variables de l'habitat échantillonnées aux échelles locale et du paysage ont été confrontées aux paramètres démographiques avec un accent particulier mis sur l'abondance et l'activité reproductrice (succès de l'appariement et de la reproduction).

Il est connu que les conditions locales d'habitat, telle la composition en essences d'arbres et la hauteur du couvert forestier ont un effet considérable sur l'abondance et le succès de reproduction de certaines espèces, cette influence variant selon les besoins vitaux de ces dernières (James et Warner, 1982; Smith et Shugart, 1987; Mazerolle et Villard, 1999). Toutefois, lorsque ces conditions forestières sont semblables, l'isolement des bois et la

distance aux grands massifs peuvent également avoir une influence déterminante sur les populations forestières. Ainsi, pour des conditions forestières locales similaires, nous posons les hypothèses suivantes:

- (1) l'abondance, le taux d'appariement et le succès de la reproduction de la Paruline couronnée diminueront en fonction de l'accroissement de la proportion de milieux agricoles au pourtour des bois et de la diminution concomitante du couvert forestier mature;
- (2) l'abondance, le taux d'appariement et le succès de la reproduction de la Paruline couronnée diminueront en fonction de la distance aux forêts continues;
- (3) le succès de nidification et le nombre moyen de jeunes produits seront affectés par une prédation et un parasitisme accrus dans les forêts les plus fragmentées.

Nous prévoyons que les paramètres démographiques (abondance, taux d'appariement et succès de la reproduction) mesurés durant cette étude varieront en fonction du contexte du paysage qui caractérise les forêts selon le gradient suivant de réponse : l'abondance, le taux d'appariement et le succès de la reproduction seront plus élevés dans les habitats contenus à l'intérieur d'un massif forestier continu que dans les habitats forestiers fragmentés de la plaine qui sont interconnectés, qui eux-mêmes présenteront de meilleurs résultats que les habitats forestiers fragmentés complètement isolés dans la matrice agricole. D'autre part, l'augmentation de la distance entre les forêts continues et les forêts fragmentées échantillonnées entraînera la diminution des trois paramètres démographiques utilisés dans l'étude.

Le premier chapitre traite de la réponse démographique de la Paruline couronnée (densité, appariement, succès reproducteur) en fonction du degré de morcellement du paysage dans le but de cibler les étapes du cycle reproducteur affectées par la fragmentation du paysage

forestier. Le deuxième chapitre examine, d'une part, les principales causes d'insuccès de nidification et discute, d'autre part, de la viabilité des populations locales de Paruline couronnée établies dans différents contextes de fragmentation.

CHAPITRE I

REPRODUCTIVE ACTIVITY OF OVENBIRDS IN A FRAGMENTED AGRICULTURAL LANDSCAPE IN SOUTHERN QUÉBEC

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Abstract: We assessed Ovenbird's reproductive activity in continuous and fragmented forests within an agricultural landscape in southern Québec, Canada. During the summers of 2004 and 2005, we monitored 225 Ovenbird territories at 20 sites. Three types of forested habitats were surveyed: a continuous forest, woodlots connected to large linear tracts and isolated woodlots. Woodlots in linear tracts and isolated woodlots were located near (< 10 km) or far (> 10 km) to a large continuous forest. Results show that the type of forest habitat did not affect Ovenbird's density and pairing success within this region. However, distance to a putative source influenced male Ovenbird's density within woodlots of linear tracts but not pairing success. The proportion of territories in which at least one young fledged was not affected by distance to a putative source but was significantly lower in woodlots of linear tracts (56.5%) and isolated woodlot (41.0%) than in the continuous forest (78.5%). Despite a high pairing success the low reproductive success in fragments of our study area indicates that reproductive activity is highly affected at the incubation and brood rearing stages. The consistency of our results over two years suggests that the continuous forest tracts may play an important role in sustaining local populations of Ovenbirds in this region.

Keywords: Fragmentation, *Seiurus aurocapillus*, abundance, pairing success, reproductive success.

Introduction

In the last decades, loss and fragmentation of habitats have been identified as major threats to forest birds that occupy human-modified landscapes in eastern North America (Robbins, 1979; Askins et al., 1990). Consequences of habitat fragmentation on avian populations include reduction in size of regional populations, increased isolation of remnant populations and reduced fecundity due to biotic processes (e.g. predation and brood parasitism) that alter local populations productivity (Whitcomb et al., 1981; Wilcove et al., 1986; Askins and Philbrick, 1987; Blake and Karr, 1987; Quinn and Harrison, 1988; Wilcove and Robinson, 1990; Rolstad, 1991; Andrén, 1994; Robinson and Wilcove, 1994). Fragmentation of breeding habitats may thus potentially affect different stages of the reproductive cycle of birds. It can cause a reduction in the abundance of territorial male birds in remnant fragments particularly where fragments are small (Robbins, 1979; Whitcomb et al., 1981; Lynch and Whigham, 1984; McIntyre, 1995). Several studies have found that pairing success is lower in small fragments that show high amounts of edge and isolation which both alter site selection and/or dispersal dynamics of females (Probst and Hayes, 1987; Villard et al., 1993; Van Horn et al., 1995; Burke and Nol, 1998). Finally, numerous studies have documented fragmentation effects on reproductive success showing that nesting failures in fragments were mainly linked to high levels of predation and brood parasitism (Donovan et al., 1995; Robinson et al., 1995a, 1995b; Donovan et al., 1997; Pomeluzi and Faaborg 1999; Burke and Nol 2000). Some of these studies have found that the landscape context, notably the amount of forest cover surrounding fragments, influenced predation and brood parasitism rates in birds nesting in woodlots of the Midwest (Robinson et al., 1995a, 1995b; Donovan et al., 1997). In fragmented landscapes of south-central Ontario, Burke and Nol (2000) have shown, however, that the amount of forest adjacent to sampled fragments had no significant effect on breeding success whereas woodlot size was the most important variable in differences in the reproductive success of several forest birds. They established the core size threshold associated with low reproductive success for Ovenbirds at approximately 23 ha. Hence, the relative contribution of patch characteristics

and landscape scale factors in forest species population parameters may vary from one region to another.

As habitat cover diminishes, isolation from putative source populations increases, which in turn has a negative effect on forest birds occurrence and densities (Van Noorden et al., 1988; Nol et al., 2005). Pairing success may also depend on dispersal and movement capability between patches of breeding habitat (Villard et al., 1993) and variations in reproductive success with distance to putative sources may be attributed to non-random dispersal among forest fragments (Villard et al., 1995). In fact, experienced breeders, which are thought to arrive on breeding grounds before younger males, may have a better chance at establishing territories in fragments near source habitats (Bayne and Hobson, 2001). These are often pictured as relatively undisturbed large woodlots, which may increase males' capability of attracting females and thus their pairing success. Furthermore, assuming that experienced males are more successful at fledging young (Holmes et al., 1996), an increased proportion of experienced males in woodlots near putative sources could also lead to an improved reproductive success. Similar hypotheses have been tested in the past, although they were not assessing distance from putative source effects. For instance, inexperienced individuals have been shown to be more abundant in poor breeding habitats (Holmes et al., 1996). However, Burke and Nol (2001) results did not support this trend. Hence, distance from continuous forests may be important to density and pairing success, and may also have a potential effect on reproductive success.

In this paper, we document variation of male density, pairing success and reproductive success in a population of Ovenbirds within continuous and fragmented forests embedded in an agricultural landscape in southern Québec. The Ovenbird is known to be sensitive to habitat interior conditions (Van Horn and Donovan, 1994). This species belongs to the neotropical migrant group and is easily detected with conspecific playbacks. Our objective was to assess fragmentation effects from two perspectives: the amount of forest cover adjacent to the sampled fragments and the distance of fragments from a putative source (a continuous forest).

More specifically, we wanted to pinpoint the stages in the reproductive cycle that were most affected by forest fragmentation. We predicted a reduction in territorial male density, pairing success and reproductive success as the proportion of forest cover surrounding the study sites becomes reduced. The same pattern was expected with respect to increased distance from the putative source (the continuous forest; > 1000 ha core area).

Methods

Study sites

Located in the St. Lawrence Lowlands, the Montérégie region is in the sugar maple-hickory stand climatic zone (Rowe, 1972). The human population for the Montérégie region is 1 400 000, making it the second most populated region in Quebec, Canada. This region was greatly altered by human-induced disturbances since colonisation when substantial site clearings occurred. Agriculture is mainly centered on field crops, livestock (cattle, pork and beef), and, to a lesser extent, on vegetable farming. Wide-row crops, mainly made up of corn, account for 69% of the cultivated territory (COVABAR, 1999). The mean regional forest cover¹ calculated with ArcView GIS 3.2 (Environmental System Research Institutes, 1996) is 16.5%. Within this landscape, 50.8% of the remnant woodlots had less than 23 ha of core area (forest > 100 m from the edge), the core size threshold associated with low reproductive success for Ovenbirds (*sensu* Burke and Nol, 2000). Woodlots with at least 23 ha in core forest area represented only 10.5% of remnant forests but hold 92.9% of the landscape's total amount of core forests.

The study sites were located in the St. Lawrence valley on both sides of the Richelieu river watershed, Québec, Canada (Figure 1.1). Twenty mature forest sites were sampled: four sites were located within the continuous and preserved forest of Mont Saint-Hilaire (UNESCO Biosphere Reserve; > 1500 ha of forest, > 1000 ha core area with a 100 m edge buffer) and sixteen sites were located in forests embedded in the agricultural matrix of the St. Lawrence valley. Of these, eight sites were sampled in woodlots connected (hereafter named «connected woodlots») to a large corridor of forests of more than 1 km wide by 40 km long. The eight others (hereafter named «isolated woodlots») were located in smaller remnants completely surrounded by the agricultural matrix. The selected stands were at least 70 years old, 17 metres in canopy height and 60% in tree density. The 16 sites were evenly distributed

¹ Forest cover within a 25 km radius from study sites.

near (< 10 km) and far (> 10 km) from our putative source (the continuous forest) (as in Beier et al., 2002). The canopy of all study sites was co-dominated by sugar maple (*Acer saccharum*), red maple (*Acer saccharinum*), beech (*Fagus grandifolia*) and eastern hemlock (*Tsuga canadensis*) whereas yellow birch (*Betula alleghaniensis*), ash (*Fraxinus* sp.), basswood (*Tilia americana*) and bitternut hickory (*Carya cordiformis*) were secondary species. These mesic to humid woodlands harboured a highly diversified flora (COVABAR, 1999). Finally, given that Ovenbird's reproductive success is negatively affected by woodlot size (Burke and Nol, 2000), particularly woodlots that have less than 23 ha of core area (forest > 100 m from the edge), most of our farm woodlots (isolated and connected) were above this core size threshold but two sites had 14 and 15 ha of core area (Table 1.1).

Local habitat and landscape context variables

Within each of the 20 selected site (11.25 ha), local features of vegetation structure and composition were quantified using 21 sampling points distributed on 7 linear transects (4 m x 60 m). We measured and calculated 21 habitat variables (Table 1.2). The linear transects were used to measure 1) tree species composition, 2) basal area and density of trees (> 8 cm DBH), and 3) basal area and density of snags (> 8 cm DBH). Sampling points were used to quantify vertical structure of the vegetation that was subdivided into four layers: ground (< 1 m), shrub (1-2 m), sapling (2-10 m), sub-canopy (10-17 m) and canopy (> 17 m). For each layer, percent cover of vegetation was estimated using a semi-quantitative scale (0-1%, 1-5%, 5-10%, 10-15%, 15-20%, etc.). General habitat features such as litter depth and presence of forest management and maple syrup production activities were also noted at each vegetation sampling point.

The landscape context around each study site was derived from digitized vegetation maps (1: 20 000). We defined three non-forest habitat types (agricultural land, urban/residential areas, and hydrologic landscape components) and three forest habitat types based on seral conditions (shrub/saplings, young forests, late-seral forests). Landscape composition variables

(proportion of agricultural land, proportion of young/mature forest, proportion of mature forest) were assessed by calculating the proportion of area occupied by each forest and non-forest habitat type within a 2 km radius circle centered on each site. Landscape configuration was measured with distance to a continuous forest. Patch-scale variables such as patch core area were also calculated from digitized vegetation maps.

Ovenbird sampling

At each site, Ovenbirds were sampled during five visits using spot mapping (Bibby, 2000) combined with song playbacks (Falls, 1981; as in Villard et al., 1993). The density of territorial males per hectare was calculated from the total number of territories per grid (300 m x 375 m; 11.25 ha). Pairing status was determined by monitoring the activities of territorial males using the methods of Villard et al. (1993). A territorial male was considered paired if it was observed with a non-singing individual (assumed to be a female) within a 5 m radius or with an individual emitting series of "tsip" notes (Lein, 1980). Territorial males that were still unaccompanied after at least 90 minutes of tracking (cumulative amount of time over 5 visits during which a bird was followed without losing visual or aural contact) (Probst and Hayes, 1987; Villard et al., 1993) and five visits were given an unpaired status. Pairing success was calculated as the proportion of paired males per site. Buford's et al. (1996) method of family group detections was applied to focal territorial males to estimate reproductive success. Territorial males that fledged at least one juvenile were considered successful. Reproductive success was calculated as the proportion of successful males per site. We completed our observations as soon as reproductive status was ascertained with confidence (i.e. when a male or a female was seen with young, or when an active nest was terminated).

In this study, male Ovenbirds were not color-banded. Nonetheless, rigorous territory mapping accomplished by three radio-equipped observers on sites using conspecific song playbacks during visits was sufficient to make us confident of territorial males' identity.

Statistical analyses

To compare treatments' main effects and their interactions, two-way ANOVA including forest type (continuous, connected and isolated) and distance from putative source (< 10 km, > 10 km) were conducted on demographic parameters male density, pairing success and reproductive success. Post-hoc Tukey's tests were used to determine which treatments differed when a statistically significant result was obtained. Percentage data were arcsin transformed for the statistical analyses.

To determine which factors were most related to variation in the three breeding parameters, we performed regression modelling on demographic parameters with respect to eight a priori models based on habitat variables known to influence Ovenbird demography. These were local vegetation cover (Robbins et al., 1989; Van Horn, 1990), local ground cover (Robbins, 1978), local forest management (Robinson and Robinson, 1999), local litter depth (Van Horn, 1990; Burke and Nol, 1998), patch core area (Temple, 1986; Burke and Nol, 2000; Bayne and Hobson, 2002), landscape agricultural cover (Bayne and Hobson, 2001, 2002), landscape mature forest cover (King et al., 1996) and distance to putative sources (Nol et al., 2005) (Table 1.3). We obtained sums of squared residuals, AIC values, coefficient signs and p-values for each candidate model in PROC REG in SAS, version 8.02 (SAS Institute, Cary, North Carolina). Akaike's Information Criterion corrected for small sample size (AIC_c; Akaike 1973; Burnham and Anderson, 2002; Mazerolle, 2004) calculated from AIC values obtained in SAS was used to compare the models and single out the best candidate model (with the lowest AIC value). As in Burnham and Anderson (2002), AIC < 2 suggests substantial evidence for the model; values between 3 and 7 indicate that the model has considerably less support, whereas models with AIC values > 10 are very unlikely to explain the response variable.

Results

Local habitat characteristics of woodlots

Comparisons of vegetation variables measured in each sampled woodlot revealed similarities and differences in the composition and structure of forest stands (Table 1.2). First, canopy height, overall vegetation cover and tree basal area were similar among treatments indicating that our selection of study sites based on forest maps criteria (> 70 years old, > 17 m in height, > 60% density) was efficient. The main differences were between the continuous forest and woodlots in the agricultural matrix. Litter depth, snag abundance and percent cover of American beech (*Fagus grandifolia*) were significantly more developed in the continuous forest than in agricultural woodlots (Table 1.2). Likewise, agricultural woodlots showed significantly more signs of forest management and human disturbances, with higher densities of small trees and higher percent cover of red maple (*Acer rubrum*) a tree species associated to disturbed sites (Brisson and Bouchard, 2003). All these differences indicated that anthropogenic activities were more conspicuous in agricultural woodlots than in the continuous forest of Mont Saint-Hilaire. Indeed, connected and isolated woodlots showed signs of management (thinning, selective logging, maple syrup production) whereas sites in the continuous forest of Mont Saint-Hilaire were located within an unmanaged old-growth forest (Leduc and Bergeron, 1998).

Landscape context characteristics

The mean amount of forest cover and agricultural cover within a 2 km radius of sampling sites were respectively 76.5% and 4.5% in the continuous forest, 33.4% and 59.0% in connected woodlots, and 10.1% and 79.3% in isolated woodlots (forest cover: ANOVA, $n = 20$, $F = 67.640$, $p < 0.001$; agricultural cover: ANOVA, $n = 20$, $F = 50.690$, $p < 0.001$; Figure 1.2). The amount of forest and agricultural cover differed between sites sampled in Mont Saint-Hilaire and farm fragments (forest cover: ANOVA, $n = 20$, $F = 25.173$, $p < 0.001$; agricultural

cover: ANOVA, $n = 20$, $F = 21.891$, $p < 0.001$; Figure 1.3). However, post-hoc Tukey's test showed no significant differences in the amount of forest and agricultural cover between farm fragments near (< 10 km) or far (> 10 km) from the putative source (Figure 1.3). Hence, controlling for this effect allowed rigorous testing of the interaction between landscape context and distance from putative source.

Annual variation in breeding birds' activity

Observations were made from 225 Ovenbird territories (112 and 113 territories in 2004 and 2005 respectively) between mid-May and mid-July. Overall, most inter-annual comparisons for male density, pairing success and reproductive success were not significant, except pairing success in sites distant from a putative source (Contingency table, $n = 76$, $X^2 = 8.830$, $p = 0.003$; Table 1.4). This did not affect, however, difference in pairing success between treatments (continuous vs. near vs. distant sites from putative source) that remained non-significant over the two years (Contingency Table, $n = 112$, $X^2 = 3.771$, $p = 0.152$ in 2004; Contingency Table, $n = 113$, $X^2 = 3.238$, $p = 0.198$ in 2005; Table 1.4). Since comparisons between treatments (forest type or distance from putative source) were consistent over years we pooled data for the two years in further analyses.

Male density

Male densities did not significantly differ between forest types whereas it varied from 0.567 male/ha in the continuous forest, to 0.506 male/ha in connected woodlots and 0.456 male/ha in isolated woodlots (ANOVA, $n = 20$, $F = 1.298$, $p = 0.272$; Figure 1.4). As shown in Table 1.5, observed male densities were similar to results published in other fragmented landscapes (Porneluzi et al., 1993; Bayne and Hobson, 2001).

Male density varied significantly in terms of distance from putative sources (ANOVA, $n = 20$, $F = 7.067$, $p = 0.018$; Figure 1.4). Interestingly, the difference in male density was significant

only for sites located far from continuous forests (> 10 km). Male densities near (< 10 km) and within continuous forest were similar (0.567 male/ha in continuous forests and 0.539 male/ha near putative sources, Figure 1.4) whereas male density in woodlots distant to putative sources was less with 0.422 male/ha (Figure 1.4). Thus, there was a significant interaction between the forest type and distance to putative source (ANOVA, $n = 20$, $F = 4.631$, $p = 0.048$; Figure 1.4). Indeed only male density within connected woodlots diminished as a function of distance to putative sources, as male density within isolated woodlots did not vary across these distance classes.

Pairing success

Pairing success was similar among forest types ranging from 94.2% in continuous forests to 87.8% in connected woodlots and to 85.4% in isolated woodlots (ANOVA, $n = 20$, $F = 1.322$, $p = 0.293$; Figure 1.5). There were no significant differences between pairing success values from different distance to putative sources (ANOVA, $n = 20$, $F = 1.186$, $p = 0.324$; Figure 1.5) and no interaction between forest type and distance to continuous forest (ANOVA, $n = 20$, $F = 2.348$, $p = 0.146$; Figure 1.5).

Reproductive success

A significant difference in reproductive success was detected among forest habitat types with higher reproductive success in the continuous forest (78.5%) and lower values in connected woodlots (56.5%) and in isolated woodlots (41.0%) (ANOVA, $n = 20$, $F = 11.196$, $p < 0.001$; Figure 1.6). The reproductive success varied significantly between sites in the continuous forest and woodlots near and far from putative sources (ANOVA, $n = 20$, $F = 3.670$, $p = 0.007$; Figure 1.6) but Tukey's post-hoc comparisons did not show significant differences between woodlots near of far from putative sources (Figure 1.6). No interaction between forest type and distance to putative sources was detected (ANOVA, $n = 20$, $F = 0.041$, $p = 0.841$; Figure 1.6).

Regression modelling

The amount of mature forest cover within a radius of 2 km came out as our best model among the candidate models analysed to explain the variation in males' densities in our study sites (Table 1.6). This model had an Akaike weight of 51.1% (Table 1.6). Distance to continuous forests, local forest management and agricultural cover followed with delta AIC_c over 3 and carrying an AIC_c weight near 12%.

Amount of agricultural cover and local ground cover carried respectively 36.1% and 22.2% of AIC_c weight for pairing success. However, the model that included all variables also had a delta AIC_c lower than two (Table 1.6). This indicates that AIC_c procedure failed to single a best model from the candidate set. Moreover, no candidate model was more parsimonious than the global model. This situation is explained by the relatively low variation in pairing success across the entire study area (Figure 1.5).

Finally, with regards to the reproductive success, the amount of agricultural cover within a 2 km radius dominated the set of candidate models, carrying 95.7% of the AIC_c weight (Table 1.6). Forest patch core area and mature forest cover were far behind with delta AIC_c above 7 and 8 respectively and carrying an AIC_c weight under 2.5%.

Discussion

Male density

The slight difference in male density between types of forests was not significant. Several studies found abundance to be negatively affected by reduced patch area or reduced proportion of forest cover in fragmented landscapes (Porneluzi et al., 1993; Donovan, 1994; Burke and Nol, 1998), thus concluding that territorial male densities might reflect the foraging quality of habitat, which is often poor in isolated woodlots. Burke and Nol (1998) showed that patches with less than 23 ha in core area should be viewed as habitats with lower food availability and with limited abundance of potential nest sites. Since most of our sampling sites, including isolated forests, were located in patches with core area above this threshold (Table 1.1), we consider that territorial males had access to habitats that offered adequate foraging conditions in all of our forest treatments.

Nonetheless, male densities across the landscape showed an interesting pattern with respect to distance from continuous forests. First, connected woodlots near continuous forests (< 10 km) had similar male densities to continuous forest. Male densities in far connected woodlots (> 10 km) had significantly lower densities that were, however, comparable to those in isolated woodlots. This variation may be related to non-random dispersal of birds among forest fragments. Indeed, smaller local populations may be a consequence of net emigration, which may be resulting from the combined effects of low survival rates of previous breeders and reduced pool of immigrants (Villard et al., 1995). Lower density in isolated woodlots and connected forests far from continuous forests could be explained by a combination of poor site fidelity due to poor quality of breeding habitat and lower immigration due to isolation from sources of dispersers (Villard et al., 1995; Porneluzi, 2003).

Mature forest cover was the best predictor variable for Ovenbird male density (Table 1.6). Distance to continuous forests, presence of forest management and percent agricultural cover within 2 km were marginally significant predictors and carried an AIC_c weight of approximately 11%. These results support our treatment analyses that showed a negative trend in male density related to the interaction between reduction in the amount of forest cover at the landscape scale and increased distance to large forests.

Pairing success

The lack of significant differences in pairing success may be interpreted in several ways. First, the sex ratio in the study area might be well balanced (Villard et al., 1993). This situation could lead females to seek for males and/or territories as far as in isolated woodlots. However, since pairing success was under 100%, even in the continuous forest, the sex ratio across the landscape is probably male-biased (Villard et al., 1993).

Second, recent studies that detected fragmentation-induced variation in Ovenbird pairing success were conducted within a range of agricultural woodlots for which size varied from small (less than 23 ha of core area, sensu Burke and Nol, 2000) to large (more than 23 ha of core area) (Gibbs and Faaborg, 1990; Villard et al., 1993; Van Horn et al., 1995; Burke and Nol 1998). In our study, the size of our agricultural woodlots varied from 44 to 232 ha and apart from two woodlots (site 33 and 44: 14.0 and 15.1 ha respectively), the majority of woodlots had core area over 23 ha. Hence, the lack of variation in pairing success among our farm woodlots could simply reflect that our sampling set was beyond the woodlot size threshold at which Ovenbird pairing success is affected.

Third, Villard et al., (1993) found that pairing success is somehow linked to male density. In their study, the male density threshold at which pairing success was affected was approximately 0.40 male per ha. Mean male density in our isolated woodlots was 0.45 male per ha. Hence, high pairing success throughout our study area may be linked to high male

densities. This may be explained by Ovenbirds tendency to seek social conspecific interactions when it is time to establish a breeding territory or to choose a mate (Van Horn and Donovan, 1994). Therefore, above a given male density threshold, disadvantages related to low amounts of forest in the landscape may be outweighed by the proximity of established conspecifics. Consequently, local male densities within a woodlot may be an important factor for females breeding site selection. As for the lack of relationship between pairing success and distance to putative sources our results indicate that isolation of woodlots does not affect the dispersal of males and females within this agricultural matrix.

Reproductive success

Our prediction that Mont Saint-Hilaire should experience a higher reproductive success than farm woodlots was supported. Moreover, regression models indicate that the landscape context surrounding these woodlots was strongly associated with their reproductive success. Ovenbirds territories in woodlots surrounded by a high proportion of agricultural land (isolated woodlots) had significantly less success than in woodlots with less agricultural land (connected woodlots). Given that pairing success was similar in these sites, our low reproductive success values are possibly linked to incubation and brood rearing stages. Predator communities and higher abundance of Brown-headed Cowbirds in isolated woodlots could be responsible for such differences. Predators are indeed more abundant in small and isolated forests (Wilcove, 1985) and in highly fragmented landscapes (Donovan et al., 1995). Therefore, nests embedded in agriculture-dominated landscapes are more likely to be depredated. It is also well known that Brown-headed Cowbird abundance has increased due to the fragmentation of North American deciduous forests. Many forest bird populations, not adapted to brood parasitism, suffer from the population increase of this open habitat species (Brittingham and Temple, 1983; Robinson et al., 1995b).

It is also known that habitat quality could affect bird reproductive capacity (Burke and Nol, 1998). Although our sampling sites were selected on the basis of mature deciduous forest

criteria (at least 70 years old, 17 m in canopy height, 60% tree density) some forest attributes differed between treatments (Table 1.2). In fact, the main factor contributing to differences in vegetation composition and structure was forest management (thinning, logging, maple syrup production). Anthropogenic activities were indeed more conspicuous in farm woodlots than in the continuous forest, which, as an old-growth deciduous forest, harboured "better" Ovenbird breeding habitat. For instance, attributes that may be related to arthropod availability such as snags and litter depth (Van Horn and Donovan, 1994; Burke and Nol, 1998) were significantly more important in the continuous forest. Therefore, lower number of territories with at least one fledgling, could result from food shortage and lower breeding habitat quality in farm woodlots (*sensu* Burke and Nol, 1998).

Regression analyses showed landscape variables to explain most of the variation in reproductive success (Table 1.6). Indeed, the amount of agricultural cover within a radius of 2 km was the main variable associated with Ovenbird reproductive success in the study area. While showing significant coefficients, the following models (patch core area, mature forest cover, litter depth, forest management) carried small AIC weights. This result corroborates our treatment analyses that showed reproductive success to be significantly lower within isolated woodlots surrounded by agriculture. This is also consistent with other findings suggesting landscape variables as important factors in the demography of forest birds (Wiens, 1994; Mazerolle and Villard, 1999; Villard, 1999; Villard et al., 1999; Lee et al., 2002). Increases in the amount of agricultural fields, which often translate into decreases in regional forest cover, are favourable to farmland-associated predators and Brown-headed Cowbird, both considered as main causes of forest bird population declines in forest landscapes modified by agriculture (Wilcove, 1985; Donovan et al., 1995; Robinson et al., 1995a; Chalfoun et al., 2002).

Burke and Nol (2000) also obtained lower reproductive success for nests in forest fragments than in continuous forests. However, woodlot size was the main explanatory variable in their study and the amount of forest cover surrounding woodlots was not a significant predictor. Forests with less than 23 ha of core area had significantly lower reproductive success than

large (> 23 ha) woodlots. In our study, we controlled for woodlot size effect and selected sites (connected and isolated) above this 23 ha threshold. Hence, our results indicate that once the woodlot size effect is taken into account the landscape context in which these larger woodlots are embedded matters.

Conclusion

Our results, along with others' (Vickery et al., 1992; Zanette, 2001), indicate that high male density and pairing success values do not necessarily translate into high local reproductive success. Hence, Ovenbirds' lower reproductive activity in fragmented forests within our study area seems to be mainly attributable to processes affecting incubation and brood rearing stages rather than dispersal, nest site selection, and pairing of males and females. Our results thus clearly point toward fragmentation effects on juvenile productivity.

Consistency in the patterns detected for the three population parameters over the two years of the study indicate that despite poor reproductive success experienced in isolated and connected woodlots, ovenbird populations throughout the landscape remain constant. Hence, a source-sink metapopulation between continuous forest such as Mont Saint-Hilaire and agricultural forests in the St. Lawrence valley is suggested. In such system, movement between local populations is a key to metapopulation viability. Since there are strong indications that breeding birds show poor site fidelity in low-production nesting habitats (Roth and Johnson, 1993; Haas, 1998; Porneluzi and Faaborg, 1999; Bayne and Hobson, 2002; Porneluzi, 2003) it is appealing to assume that repeated high bird density within these habitats is directly linked to recruitment and dispersal from source habitats.

Our coarse indicator of reproductive success (presence of fledglings in territories with a territorial male) showed that continuous forests was a better breeding habitat than fragmented forests, particularly isolated woodlots where small proportions of habitat cover are entirely embedded within the agricultural matrix. This raises several questions on the long-term viability

of isolated woodlot populations in this study area and its dependence on continuous forests juvenile production. The exact role of continuous forest tracts with regards to regional population dynamics of forest interior species such as Ovenbirds will require more in depth demographic studies that imply direct nest monitoring (Burke and Nol, 2000; Bourque and Villard, 2001) and capture-recapture studies of individuals dispersal at the landscape scale (Bayne and Hobson, 2002). Finally improving our understanding about causal factors associated with reproductive failure will require more research on productivity centered on direct nest monitoring. Potential causal factors include predation and brood parasitism (Donovan et al., 1995; Pomeluzi and Faaborg, 1999; Burke and Nol, 2000), poor foraging habitat (Burke and Nol 1998; Zanette, 2001) and inexperience of adults (Holmes et al., 1996) in agricultural woodlots.

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Tables and figures

Figure 1.1 Map of the study area located in southern Québec, Canada.

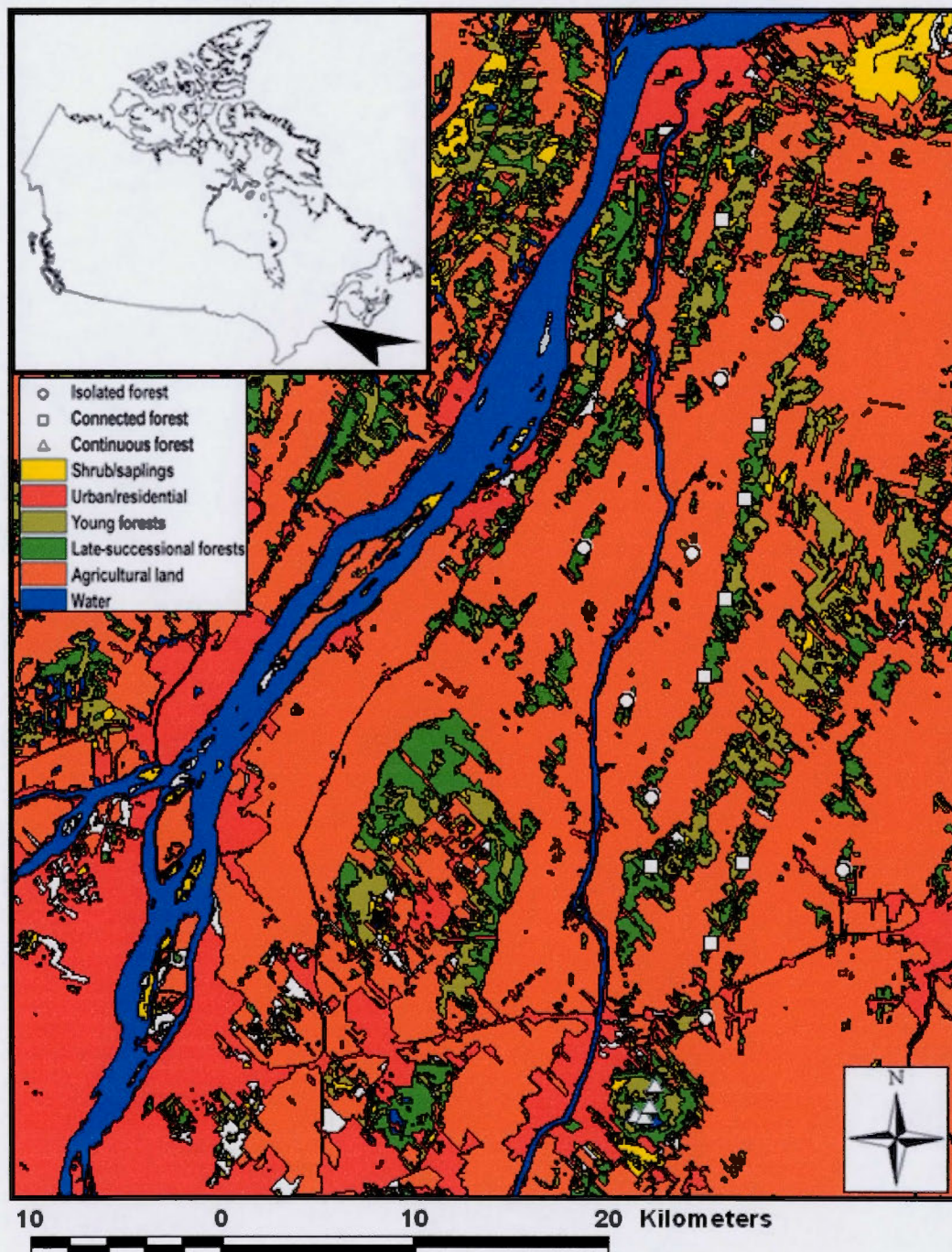


Table 1.1 Description of study sites in southern Québec, Canada.

<i>Study site</i>	<i>Habitat type</i>	<i>Distance to continuous forests¹</i>	<i>Agr. cover² (%)</i>	<i>Distance³ (m)</i>	<i>Total area⁴ (ha)</i>	<i>Core area⁵ (ha)</i>
11	Connected woodlot	Near	35.5	6352	1932.2	364.8
12	Connected woodlot	Near	73.4	6262	360.8	27.3
13	Isolated woodlot	Near	56.7	2688	174.7	73.9
24	Isolated woodlot	Near	80.1	6074	232.9	65.0
21	Connected woodlot	Near	74.0	8388	1004.6	612.0
22	Connected woodlot	Near	62.8	9356	260.2	136.6
23	Isolated woodlot	Near	85.6	7928	86.2	42.6
34	Isolated woodlot	Near	81.5	9526	209.2	114.8
31	Connected woodlot	Far	56.7	14741	1004.6	612.0
32	Connected woodlot	Far	54.2	18492	1295.1	854.4
33	Isolated woodlot	Far	86.2	14620	63.1	14.0
14	Isolated woodlot	Far	79.8	13067	81.1	40.9
41	Connected woodlot	Far	68.0	21605	1295.1	854.4
42	Connected woodlot	Far	47.4	28934	2345.2	665.6
43	Isolated woodlot	Far	76.8	26541	57.5	23.6
44	Isolated woodlot	Far	87.5	22358	44.3	15.1
M1	Continuous forest	-	0.4	-	1532.8	1051.2
M2	Continuous forest	-	1.8	-	1532.8	1051.2
M3	Continuous forest	-	3.6	-	1532.8	1051.2
M4	Continuous forest	-	12.4	-	1532.8	1051.2

¹ Near: <10 km from a continuous forest (>1000 ha core area) ; Far: > 10 km from a continuous forest.

² Proportion of agricultural cover within 2 km radius of sampling site.

³ Distance in meters from forest edge to a continuous forest (> 1000 ha core area).

⁴ Total area of forest patch.

⁵ Area of core forest patch containing study site, considering an edge buffer of 100 meters.

Table 1.2 Variation of local habitat characteristics (Mean \pm SE) between stands within the continuous forest, connected woodlots and isolated woodlots (One-way ANOVA). Within 20 study sites, forest composition variables were calculated from data sampled from seven transects (60 m x 4 m) whereas other characteristics were measured at 21 vegetation-sampling points (isolated woodlots, n = 8; connected woodlots, n = 8; continuous forest, n = 4).

	<i>Isolated woodlots</i>		<i>Connected woodlots</i>		<i>Continuous forest</i>		<i>F (P)</i>
	<i>Mean</i>	<i>SE</i>	<i>Mean</i>	<i>SE</i>	<i>Mean</i>	<i>SE</i>	
<i>Forest composition</i>							
<i>Acer saccharum</i> basal area (m ² /ha)	14.5	3.7	14.3	3.7	15.3	5.2	0.090 (0.914)
<i>Acer rubrum</i> basal area (m ² /ha)	12.6	2.0	14.0	2.0	0.5	2.8	8.464 (0.003)
<i>Fagus grandifolia</i> basal area (m ² /ha)	3.0	1.3	8.5	1.3	15.3	1.9	14.829 (<0.001) ³
<i>Tsuga canadensis</i> basal area (m ² /ha)	3.4	1.4	7.8	1.4	<0.1	1.9	5.920 (0.011)
<i>Forest structure</i>							
Tree basal area (m ² /ha)	45.2	3.1	50.7	3.1	37.8	4.4	2.946 (0.080)
Snag basal area (m ² /ha)	1.3	0.4	1.2	0.4	6.8	0.6	19.900 (<0.001)
Tree density, DBH 8-14cm (nb/ha)	424.9	42.1	328.1	42.1	247.0	59.5	3.464 (0.055)
Tree density, DBH 15-29cm (nb/ha)	452.4	33.9	410.7	33.9	244.0	47.9	6.498 (0.008)
Tree density, DBH >29cm (nb/ha)	200.1	19.7	242.6	19.7	181.5	27.9	1.966 (0.171)
Snag density, DBH 8-14cm (nb/ha)	35.7	7.5	25.3	7.5	11.9	10.6	1.716 (0.210)
Snag density, DBH 15-24cm (nb/ha)	15.6	3.9	11.2	3.9	34.2	5.5	6.127 (0.010)
Snag density, DBH >24cm (nb/ha)	6.0	3.7	4.5	3.7	52.1	5.2	18.096 (<0.001)
Mean DBH (cm)	20.6	0.9	22.5	0.9	22.9	1.2	1.722 (0.209)
Canopy height (m)	20.9	0.6	22.9	0.6	21.7	0.9	2.599 (0.104)
Sapling cover (2-10m; %)	30.2	1.8	29.9	1.8	41.4	2.6	7.641 (0.004)
Shrub cover (1-2m; %)	10.1	1.4	5.6	1.4	13.3	2.0	5.682 (0.013)
Vegetation cover (1m-canopy; %)	71.5	2.3	70.9	2.3	79.8	3.3	3.003 (0.076)
Ground cover (<1m; %)	39.1	4.7	36.1	4.7	22.4	6.6	2.101 (0.153)
Litter depth (mm)	85.8	3.6	88.7	3.6	145.8	5.1	38.498 (<0.001)
<i>Perturbation indices</i>							
Forest management ¹ (%)	50.9	2.7	51.2	2.7	0.6	3.9	55.670 (<0.001)
<i>Acer</i> management ² (%)	31.5	8.5	49.4	8.5	0.0	12.0	4.853 (0.022)

¹ Proportion of vegetation-sampling points within study sites showing signs of logging activities.

² Proportion of vegetation sampling points within study sites showing signs of maple syrup production activities.

³ *Fagus grandifolia* basal area: Only local variable showing a significant difference between connected and isolated woodlots (posthoc Tukey's HSD, $p = 0.024$).

Table 1.3 Description of variables used for generalized linear models.

<i>Variable</i>	<i>Description</i>
Local habitat	
Local vegetation cover	Mean proportion of vegetation cover (1m-canopy) (%)
Local ground cover	Mean proportion of ground covered with vegetation (%)
Local forest management	Logging index ¹ (%)
Local litter depth	Mean litter depth (mm)
Landscape cover	
Patch core area	Area of core forest containing a study site (100 m edge buffer; ha)
Agricultural cover	Proportion of agricultural land in a 2 km radius (%)
Mature forest cover	Proportion of mature forest in a 2 km radius (%)
Distance to continuous forests	Distance to closest forest of > 1000 ha in core area (m)

¹ Calculated from logging presence/absence at each vegetation sampling points within study sites.

Figure 1.2 Mean proportions (\pm SE) of forest and agricultural cover in a 2 km radius around sampling sites for each type of forest habitat (forest cover: $n = 20$, $F = 67.640$, $p < 0.001$; agricultural cover: $n = 20$, $F = 50.690$, $p < 0.001$; *** $p < 0.001$).

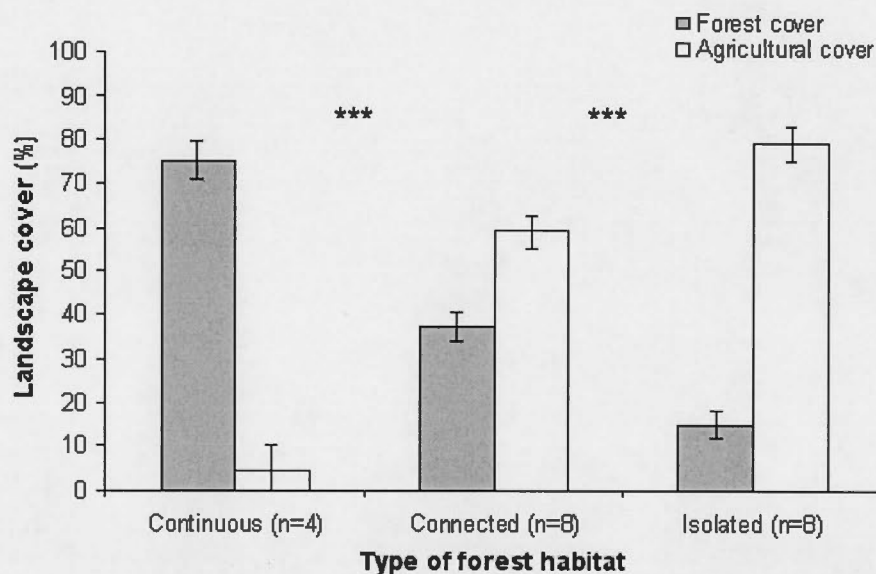


Figure 1.3 Mean proportions (\pm SE) of forest and agricultural cover in a 2 km radius around sampling sites in the continuous forest, connected and isolated woodlots near (< 10 km), and connected and isolated woodlots far (> 10 km) from continuous forests (forest cover: $n = 20$, $F = 25.173$, $p < 0.001$; agricultural cover: $n = 20$, $F = 21.891$, $p < 0.001$; *** $p < 0.001$).

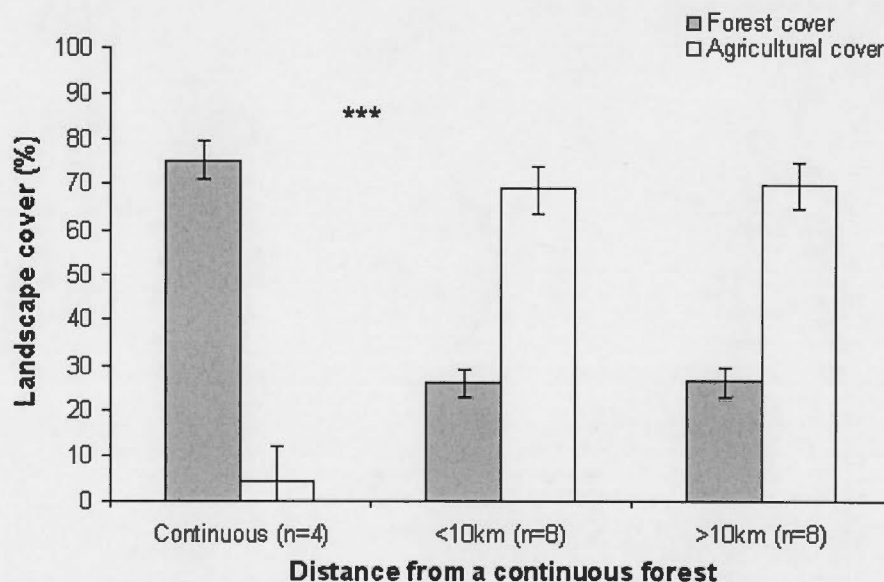


Table 1.4 Annual variation of Ovenbird male density, pairing success and reproductive success with respect to forest type and distance to continuous forests.

	2004 (n)	2005 (n)	Statistic ¹	P
<i>Type of forest habitat</i>				
Male density (nb/ha)				
Isolated woodlots	0.467 (8)	0.444 (8)	0.137	0.717
Connected woodlots	0.500 (8)	0.511 (8)	0.020	0.889
Continuous forest	0.556 (4)	0.578 (4)	0.429	0.537
F, p	0.943, 0.409	1.152, 0.340		
Pairing success (%)				
Isolated woodlots	90.5 (42)	78.1 (41)	2.476	0.116
Connected woodlots	93.3 (45)	82.6 (46)	2.547	0.111
Continuous forest	96.0 (25)	92.3 (26)	0.320	0.572
χ^2 , p	0.781, 0.677	2.597, 0.273		
Reproductive success (%)				
Isolated woodlots	33.3 (42)	48.8 (41)	2.056	0.152
Connected woodlots	51.1 (45)	65.2 (46)	1.868	0.172
Continuous forest	72.0 (25)	84.6 (26)	1.210	0.271
χ^2 , p	9.753, 0.008	9.458, 0.009		
<i>Distance to continuous forests</i>				
Male density (nb/ha)				
Far (> 10 km)	0.433 (8)	0.411 (8)	0.168	0.688
Near (< 10 km)	0.533 (8)	0.544 (8)	0.024	0.880
Continuous forest	0.556 (4)	0.578 (4)	0.429	0.537
F, p				
Pairing success (%)				
Far (> 10 km)	97.4 (39)	75.7 (37)	8.830	0.003
Near (< 10 km)	87.5 (48)	84.0 (50)	0.246	0.620
Continuous forest	96.0 (25)	92.3 (26)	0.320	0.572
χ^2 , p	3.771, 0.152	3.238, 0.198		
Reproductive success (%)				
Far (> 10 km)	41.0 (39)	56.8 (37)	1.888	0.169
Near (< 10 km)	43.8 (48)	58.0 (50)	1.997	0.158
Continuous forest	72.0 (25)	84.6 (26)	1.210	0.271
χ^2 , p	6.989, 0.030	7.068, 0.029		

¹ ANOVA F statistic for male density; Contingency table analysis Chi-square statistic for pairing success and reproductive success.

Figure 1.4 Mean male Ovenbird density (\pm SE) in the continuous forest, connected woodlots and isolated woodlots for sites near (< 10 km) and far (> 10 km) from continuous forests ($n = 20$, $F = 4.631$, $p = 0.048$). (Type of forest: $n = 20$, $F = 1.298$, $p = 0.272$; Distance from continuous forest: $n = 20$, $F = 7.067$, $p = 0.018$; Categories with the same letter are not different, $p < 0.05$, Tukey's HSD).

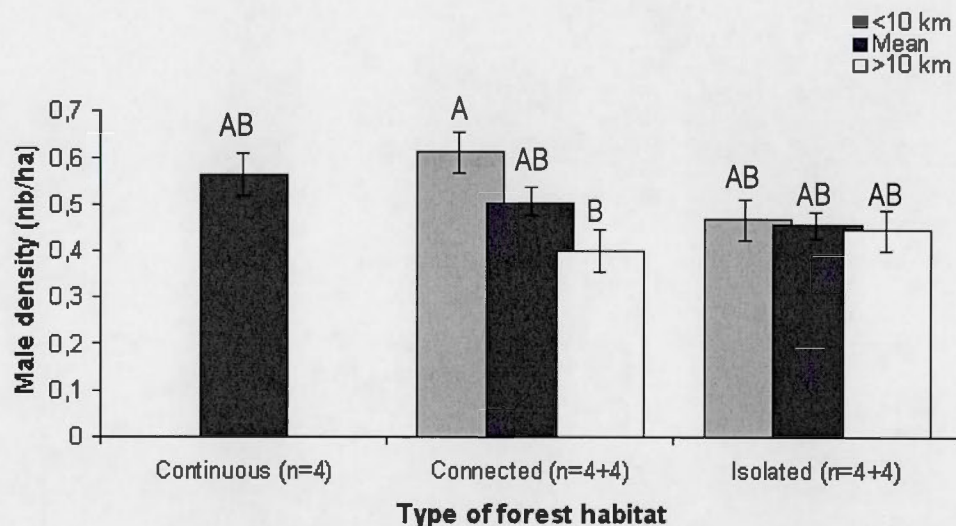


Figure 1.5 Mean Ovenbird pairing success (\pm SE) in the continuous forest, connected woodlots and isolated woodlots for sites near (< 10 km) and far (> 10 km) from continuous forests, and showing no significant interaction between type of forest and distance to continuous forests (interaction term, $n = 20$, $F = 2.348$, $p = 0.146$; Type of forest: $n = 20$, $F = 1.322$, $p = 0.293$; Distance to continuous forest: $n = 20$, $F = 1.186$, $p = 0.324$; No categories are different, $p < 0.10$, Tukey's HSD).



Figure 1.6 Mean Ovenbird reproductive success (\pm SE) in the continuous forest, connected woodlots and isolated woodlots for sites near (< 10 km) and far (> 10 km) from continuous forests, and showing no significant interaction between type of forest and distance to continuous forests (interaction term, $n = 20$, $F = 0.041$, $p = 0.841$) (Type of forest: $n = 20$, $F = 11.196$, $p < 0.001$; Distance to continuous forest: $n = 20$, $F = 3.670$, $p = 0.007$; Categories with the same letter are not different, $p < 0.10$, Tukey's HSD).

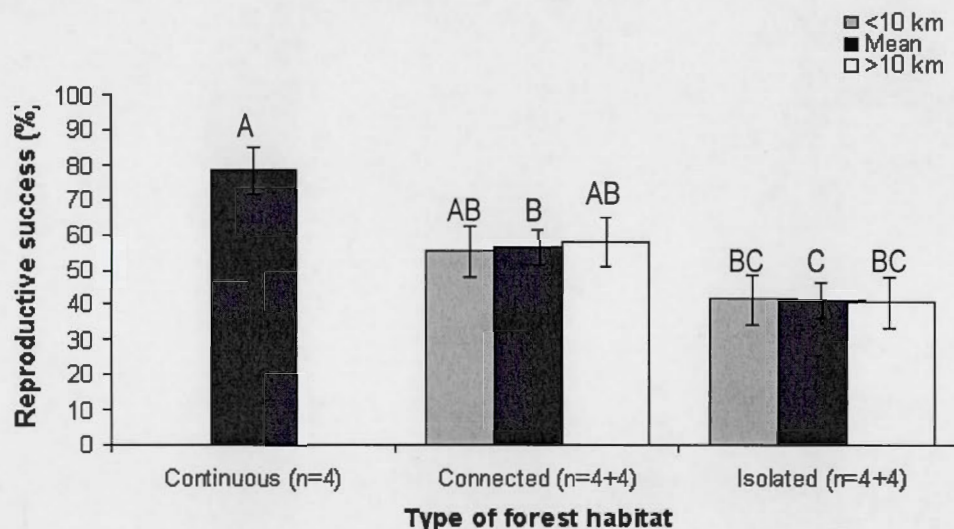


Table 1.5 Description of variables used for generalized linear models.

State/province	Male density (nb/ha)	Forest patch area (ha)	Reference
Missouri	0.14	9 - 140	Gibbs and Faaborg 1990
Missouri	0.22	>500	Gibbs and Faaborg 1990
Missouri	0.16	2020 - 4060	Porneluzi and Faaborg 1999
Ontario	0.23	4.5 - 29.5	Villard et al., 1993
Ontario	0.03 - 0.83	11.75 - 2352.75	Burke and Nol 1998
Saskatchewan	0.52	5 - 42	Bayne and Hobson 2001
Pennsylvania	0 - 0.68	9.2 - 183.2	Porneluzi et al., 1993
Pennsylvania	0.69	>10000	Porneluzi et al., 1993
Québec	0.456	44.3 - 232.9	This paper (isolated woodlots)
Québec	0.506	260.2 - 1932.2	This paper (connected woodlots)
Québec	0.567	1532.8	This paper (continuous forest)

Table 1.6 Generalized linear models for Ovenbird male density and reproductive success.

<i>Model</i>	<i>Coefficient sign (P value)</i>	<i>K¹</i>	<i>SSE²</i>	<i>AICc³</i>	<i>Δ AIC⁴</i>	<i>AICc Weight⁵</i>	<i>r²adj</i>
<i>Male density</i>							
1. Mature forest cover	+(0.015)	2	0.1703	-90.608	0	0.511	0.249
2. Distance to continuous forests	-(0.066)	2	0.1974	-87.665	2.943	0.117	0.130
3. Local forest management	-(0.067)	2	0.1975	-87.645	2.963	0.116	0.129
4. Agricultural cover	-(0.069)	2	0.1982	-87.582	3.025	0.113	0.126
5. Local litter depth	+(0.144)	2	0.2119	-86.240	4.368	0.058	0.066
6. Local vegetation cover	+(0.250)	2	0.2220	-85.309	5.299	0.036	0.021
7. Local ground cover	+(0.401)	2	0.2300	-84.605	6.003	0.025	-0.014
8. Patch core area	+(0.435)	2	0.2312	-84.495	6.113	0.024	-0.020
9. Global	-	9	0.0917	-71.696	18.912	<0.001	0.338
10. Null	-	1	5.1950	-24.738	65.869	<0.001	-
<i>Pairing success</i>							
1. Agricultural cover	-(0.017)	2	1.0388	-54.448	0	0.361	0.237
2. Local ground cover	-(0.028)	2	1.0903	-53.480	0.968	0.222	0.200
3. Global	-	9	0.2295	-53.350	1.098	0.209	0.724
4. Patch core area	+(0.072)	2	1.1952	-51.642	2.806	0.089	0.123
5. Mature forest cover	+(0.206)	2	1.3124	-49.772	4.676	0.035	0.037
6. Local litter depth	+(0.256)	2	1.3356	-49.421	5.027	0.029	0.019
7. Local forest management	-(0.441)	2	1.3898	-48.625	5.823	0.020	-0.020
8. Distance to continuous forests	-(0.467)	2	1.3949	-48.552	5.896	0.019	-0.030
9. Local vegetation cover	+(0.592)	2	1.4142	-48.277	6.171	0.017	-0.038
10. Null	-	1	5.1950	-24.738	29.710	<0.001	-
<i>Reproductive success</i>							
1. Agricultural cover	-(<0.001)	2	0.3588	-75.707	0	0.957	0.672
2. Patch core area	+(<0.001)	2	0.5196	-68.302	7.404	0.024	0.525
3. Mature forest cover	+(<0.001)	2	0.5374	-68.337	8.076	0.017	0.509
4. Local litter depth	+(0.003)	2	0.6984	-62.388	13.318	0.001	0.362
5. Local forest management	-(0.004)	2	0.7169	-61.465	13.842	0.001	0.345
6. Local ground cover	-(0.045)	2	0.9185	-56.910	18.797	<0.001	0.160
7. Distance to continuous forests	-(0.048)	2	0.9234	-57.508	18.904	<0.001	0.156
8. Local vegetation cover	+(0.224)	2	1.0610	-54.025	21.682	<0.001	0.030
9. Global	-	9	0.2561	-51.156	24.551	<0.001	0.617
10. Null	-	1	5.1950	-24.738	50.966	<0.001	-

¹ Number of parameters including the intercept.² Sum of squared residuals³ Akaike's Information Criterion corrected for small sample size.⁴ Increase in AICc over the lowest observed value of AICc.⁵ Akaike weight, strength of evidence that the model is best of the set.

CHAPITRE II

NESTING SUCCESS AND POPULATION DYNAMICS OF OVENBIRDS IN A FRAGMENTED AGRICULTURAL LANDSCAPE: INFLUENCE OF LOCAL AND LANDSCAPE SCALE FACTORS

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Abstract: We assessed Ovenbird's nesting success in continuous and fragmented forests within an agricultural landscape in southern Québec, Canada. During the summers of 2004 and 2005, we monitored 35 Ovenbird nests. Three types of forested habitats were surveyed: a continuous forest, woodlots connected to large linear tracts and isolated woodlots. Despite that forests in the fragmented landscape were large (core area >23 ha), our results showed that Ovenbird's nesting success and fledgling success were negatively affected by forest fragmentation. Most nests in isolated and connected forests of the agricultural landscapes experienced either predation, cowbird parasitism or both. The local populations in these habitats did not produce enough fledglings to maintain stable populations and thus depended on recruitment of individuals from nearby source populations. Our results suggest that the regional persistence of Ovenbirds in the St. Lawrence valley may strongly be contingent on remaining continuous forest tracts given the low capacity of forest fragments, even those that comprise large amounts of core area (> 23 ha).

Keywords: Fragmentation, *Seiurus aurocapillus*, nesting success, predation, parasitism, source-sink dynamics.

Introduction

Patterns of habitat occupancy of forest birds in fragmented habitats have been studied extensively in North American deciduous forest landscapes over the last two decades (Whitcomb et al., 1981; Blake and Karr, 1987; Robbins et al., 1989; Robinson et al., 1995b; Donovan and Flather, 2002; Burke and Nol, 2000). Several studies have clearly showed that forest bird populations using remnant fragments are highly exposed to adverse factors that jeopardize their long-term viability (Donovan et al., 1995; Robinson et al., 1995b; Burke and Nol, 2000). Among those, changes in the predator community and higher abundance of some predators in agricultural landscapes induce high levels of nest predation (Donovan et al., 1995; Bayne and Hobson, 1997; Chalfoun et al., 2002a). In such landscapes, predation is considered the main cause of nesting failure (Wilcove, 1985; Heske et al., 2001; Chalfoun et al., 2002b) and directly affects reproductive output of local populations (Donovan et al., 1995; Perneluzi and Faaborg, 1999; Burke and Nol, 2000). Brown-headed Cowbird's (*Molothrus ater*) brood parasitism is also known to substantially reduce the productivity of some forest bird species, notably those that have not coevolved with obligate brood parasites (Brittingham and Temple, 1983; Lowther, 1993; Donovan et al., 1995; Robinson et al., 1995a). Cowbirds are now abundant in Eastern North America and are thought to represent a threat to local populations established in forest habitats adjacent to agricultural land and other human-dominated landscapes (Brittingham and Temple, 1983; Donovan et al., 1995; Robinson et al., 1995b). Moreover, since these factors often co-occur in fragmented agricultural landscapes, cowbird parasitism and predation may further affect forest birds' fecundity by exerting cumulative effects on their reproductive success (Robinson et al., 1995b, Donovan et al., 1997; Burke and Nol, 2000).

Low reproductive success of forest birds may also result from inadequate foraging in fragmented forests (Burke and Nol, 1998; Zarette et al., 2000). Altered local vegetation modifies microclimatic conditions within small fragments (for instance, humidity and light levels) (Lee, 1987; Saunders et al., 1991), which may have an effect on the leaf litter fauna and food

availability of forest birds (Wenny, 1989; Burke and Nol, 1998; Zanette et al., 2000). Such conditions may either translate into a higher risk of starvation for nestlings or higher predation risk due to longer periods of nest unattendance because adults spend more time searching for food (Zanette et al., 2000; Mattsson and Niemi, 2006).

The relative importance of these causal factors is contingent on patch characteristics of remnants, such as size (Wilcove 1985; Weinberg and Roth, 1998; Burke and Nol, 2000; Chalfoun et al., 2002b), amount of edge (Flaspohler et al., 2001; Chalfoun et al., 2002a), local vegetation structure and composition for nest concealment (Huhta et al., 1996; Morse and Robinson, 1999), leaf litter depth and arthropod biomass within territories (Burke and Nol, 1998; Mattsson and Niemi, 2006). However, predation or parasitism within agricultural forest patches may also be affected by factors that occur at landscape and regional scales (Robinson et al., 1995b; Donovan et al., 1997). Hence, the landscape context in which remnants are embedded matters (Robinson et al., 1995b; Drapeau et al., 2000; but see Burke and Nol, 2000). Levels of predation and brood parasitism are known to be more important when the proportion of agricultural land is high and amount of surrounding forest (both total area and core area) is low (Donovan, 1994; Donovan et al., 1997; Hobson and Bayne, 2000; Rodewald 2002).

Productivity of populations within remnants is thus often at levels of population sinks, where poor fecundity does not allow a balance between adult mortality and juvenile recruitment (Pulliam, 1988; Donovan et al., 1995; Brawn and Robinson, 1996; Porneluzi and Faaborg, 1999; Burke and Nol, 2000). In such breeding habitats, long-term persistence of populations depends more on recruitment of individuals produced in other less fragmented areas (source population sensu Pulliam, 1988) than on local productivity.

In a previous study (chapter 1), we used indicators such as pairing success and family groups to assess the reproductive performance of breeding territorial Ovenbirds (*Seiurus aurocapillus*) in fragmented woodlots of the St. Lawrence valley region in southern Québec. While pairing

success was similar throughout the study area, we found that significantly more family groups were detected among territorial birds in continuous forest, and within fragmented habitats for connected forest fragments (linked to a forest corridor) to be more successful than isolated fragments (those embedded in an agricultural matrix). Hence, the estimated reduction in fecundity in fragmented forests in our study design was more likely to point towards nest failures during the incubation and brood rearing stages than in the first steps of the breeding cycle i.e., adult dispersal and pairing of males and females in fragmented woodlots.

In this chapter we determine the underlying causes of fragmentation effect observed with reproductive performance indirect indices used in chapter 1 by conducting direct monitoring of nests in fragmented forests (surrounded by corn fields or linked with corridors) and in a continuous forest (Mont Saint-Hilaire, a UNESCO Biosphere Reserve) in the St. Lawrence valley in southern Québec. More specifically, the objectives of our study were two-fold. First, we measured nesting success of birds and determined throughout the breeding cycle the causes of nest failure. Second, we assessed the viability of local populations established in the forest fragments surrounded by different landscape contexts and in a large continuous forest. We predicted that predation and brood parasitism would be higher and nesting success would be lower in isolated forest fragments surrounded by a larger proportion of agricultural land than in connected fragments linked to forest corridors and in the continuous forest. We also predicted that local populations established in forests fragmented by agriculture would act as population sinks and, should therefore be considered as unviable without recruitment from surrounding source populations.

Methods

Study sites

This study was conducted in the St. Lawrence lowlands, more specifically in the Montérégie region (Figure 2.1). The human population for the Montérégie region is 1 400 000, making it the second most populated region in Quebec, Canada. The region is in the sugar maple-hickory stand climatic zone (Rowe, 1972) and was greatly altered by human-induced disturbances since colonisation when substantial site clearings occurred. Agriculture is mainly centered on field crops, livestock (cattle, pork and beef), and, to a lesser extent, on vegetable farming. Wide-row crops, mainly made up of grain corn, accounts for 69% of the cultivated territory (COVABAR, 1999). The mean regional forest cover² calculated with ArcView GIS 3.2 (Environmental System Research Institutes, 1996) is 16.5%. Within this landscape, 50.8% of the remnant woodlots had less than 23 ha of core area (forest > 100 m from the edge), the core size threshold associated with low reproductive success for Ovenbirds (*sensu* Burke and Nol, 2000). Woodlots with at least 23 ha in core forest area represented only 10.5% of remnant forests but hold 92.9% of the landscape's total amount of core forests.

The study sites were located in the St. Lawrence valley on both sides of the Richelieu river watershed, Québec, Canada. Site selection was based on four criteria: canopy height and density in forest fragments, distance of fragments to continuous forest tracks, and fragment size. The selected stands were at least 70 years old, 17 m in height with tree density > 60%. The canopy of all study sites was co-dominated by sugar maple (*Acer saccharum*), red maple (*Acer saccharinum*), beech (*Fagus grandifolia*) and eastern hemlock (*Tsuga canadensis*) whereas yellow birch (*Betula alleghaniensis*), ash (*Fraxinus* sp.), basswood (*Tilia americana*) and bitternut hickory (*Carya cordiformis*) were secondary species. These mesic to humid woodlots harboured a highly diversified flora (COVABAR, 1999). Sites were also distributed within the agricultural land base to cover a range of distances within and above 10 km from a

² Forest cover within a 25 km radius from study sites.

continuous forest. Finally, to control for the effect of woodlot size on ovenbirds reproductive success we used Burke and Nol (2000) woodlot size threshold of 23 ha of core area, (forest > 100 m from the edge). Hence, apart two sites that had 14 and 15 ha of core area all other forest fragments (isolated and connected) were above this threshold (Table 2.1). Overall, twenty mature forest sites were sampled. Four sites were located within the continuous (> 1 500 ha of forest and 1 000 ha of core area with a 100 m edge buffer) preserved forest of Mont Saint-Hilaire, a UNESCO Biosphere Reserve where a large proportion is composed of unmanaged old-growth forest (Leduc et al., 1998). Sixteen sites were located in continuous forests embedded in the agricultural matrix of the St. Lawrence valley. Of these, eight sites were sampled in woodlots connected (hereafter named «connected woodlots») to a large corridor of forests of more than 1 km wide by 40 km long. The eight others (hereafter named "isolated woodlots") were located in forest remnants completely surrounded by the agricultural matrix.

Local habitat and landscape context variables

Within each of the 20 selected site (11.25 ha), local features of vegetation structure and composition were quantified using 21 sampling points distributed on 7 linear transects (4 m x 60 m). We measured and calculated 21 habitat variables (Table 2.2). The linear transects were used to measure 1) tree species composition, 2) basal area and density of trees (> 8 cm DBH), and 3) basal area and density of snags (> 8 cm DBH). Sampling points were used to quantify vertical structure of the vegetation that was subdivided into four layers: ground (< 1 m), shrub (1-2 m), sapling (2-10 m), sub-canopy (10-17 m) and canopy (> 17 m). For each layer, percent cover of vegetation was estimated using a semi-quantitative scale (0-1%, 1-5%, 5-10%, 10-15%, 15-20%, etc.). General habitat features such as litter depth and presence or absence of forest management and maple syrup production activities were also noted at each vegetation sampling point.

The landscape context around each study site was derived from digitized vegetation maps (1:20 000). We defined three non-forest habitat types (agricultural land, urban/residential areas, and hydrologic landscape components) and three forest habitat types based on seral conditions (shrub/saplings, young forests, and late-seral forests). Landscape composition variables (proportion of agricultural land, proportion of young/mature forest, proportion of mature forest) were assessed by calculating the proportion of area occupied by each forest and non-forest habitat type within a 2 km radius circle centered on each site. Landscape configuration was measured with distance to a continuous forest. Patch-scale variables such as patch core area were also calculated from digitized vegetation maps.

Ovenbird sampling

At each site, Ovenbirds densities were determined by territory mapping of singing males (Bibby, 2000) within grids of 11.25 ha placed in the core area of each woodlot (see Chapter I for territory monitoring details) for a total of five visits. We used song playbacks (Falls, 1981; Villard et al., 1993) of singing males to track territorial males and determine their pairing status. We conducted an intensive and systematic search for nests on the 197 territories occupied with paired Ovenbirds (104 territories with a pair over 112 in 2004 and 93 territories with a pair over 113 in 2005) between mid-May and mid-July. The nest search resulted in the finding of 35 nests over the two years of the study. Most nests were found incidentally during our playback sessions when following singing males and females. When they were discovered, nests were located with flagging tape at 3 m from the nest as in Bourque and Villard (2001).

If the nest was located before the first egg was laid, we considered the first observation day as the first day of egg laying. Each nest was checked every 3-5 days and nest contents were recorded. Nests were monitored until fledging or until failure occurred. We considered each nest's fate as successful (at least one host young fledged) or failed (no host young fledged). Failed nests were either considered depredated (nests in which eggs or nestlings disappeared) or abandoned (eggs or nestlings that were left unattended in nest for at least two nest checks).

Events of parasitism (one or more Brown-headed Cowbird eggs or fledglings in the nest) and partial predation (brood loss with at least one host young remaining in the nest) were also noted. Occurrences of avian and mammalian predators were also noted on every visit at our study sites. Hence, abundance of avian (Blue Jay, American Crow, Brown-headed Cowbird, raptors), and mammalian (Red Squirrel, Eastern Chipmunk, Gray Squirrel, Raccoon) predators is presented as the mean number of occurrences per visit. We used this index as a rough indicator of predator abundance in our study sites.

Daily nest mortality and nest success

We followed Donovan et al., (1995) to calculate daily nest mortality and nesting success based on the Mayfield estimate (Mayfield, 1961, 1975) and Johnson's standard error estimate (Johnson, 1979). For each forest habitat (continuous, agricultural isolated and agricultural connected) daily mortality rates were computed across the breeding cycle as total number of failures divided by total number of observation days pooled across all monitored nests. Overall nest success was based on estimate of daily success ($1 - \text{daily mortality}$) raised to the exponent that reflects average length of the entire breeding cycle within each forest habitat (Donovan et al., 1995; Burke and Nol, 2000). Johnson's chi-square comparison test (1990) was used to compare daily mortality rates (Bourque and Villard, 2001).

The effects of factors that limit reproductive success in fragmented landscapes were quantified with cause-specific daily mortality rates. These were expressed as total number of failures because nest predation and abandonment divided by total number of observation days. Because they were not responsible for nest mortality in our sample, brood parasitism and stochastic events were not included as such. Because the Mayfield approach does not apply to parasitism (equal chance of finding unparasitized and parasitized nests, as opposed to predated nests), only apparent rate is presented for parasitism (number of parasitized nests divided by total number of nests; Mayfield, 1961; Johnson and Schaffer, 1990; Burke and Nol, 2000). We assumed a 1:1 sex ratio among fledglings. Thus, number of fledglings per nest was

divided by two and averaged over landscape context in order to calculate number of female young per successful nest. We calculated annual fecundity (mean number of female young per adult female per year) from the mean number of female young produced per successful nest, population specific estimates of nest success, the number of potential renesting attempts, and the number of potential broods per season (as in Donovan et al., 1995). We assumed that female Ovenbirds could fledge a maximum of one brood per year and that females would renest once if their first attempt failed.

The Mayfield estimates of daily nest survival do not account for partial nest losses that may occur as a result of brood parasitism and/or partial predation, although that may significantly affect forest songbird populations by reducing number of host nestlings per nest (Burke and Nol, 2000). Therefore, from successful nests, we compared mean number of fledged young in nonparasitized and parasitized nests using ANOVA. The same procedure was used regarding partial predation that we defined as the partial loss of a host brood. Presence/absence of parasitism and total predation were fitted against cowbird and predator abundances (as noted in each visit) and analysed using a logistic fit.

To further investigate which environmental factors were most associated with observed nesting failure, predation, and parasitism rates, we performed regression models on habitat variables known to influence Ovenbird's demography, at stand level (Robbins, 1978; Robbins et al., 1989; Van Horn, 1990; Burke and Nol, 1998; Robinson and Robinson, 1999), forest patch level (Temple, 1986; Burke and Nol, 2000; Bayne and Hobson, 2002), and at the landscape level (King et al., 1996; Donovan et al., 1997; Bayne and Hobson, 2001, 2002; Nol et al., 2005). Explanatory variables used in regression models are described in Table 2.3. Response variables represented "presence/absence" data type and corresponded to 1) "Nest failure" that shows the effect of total predation and nest abandonment combined, 2) "Nest parasitism" (probability of a nest being parasitized by a Brown-headed Cowbird) and 3) "Nest predation" which relates to the probability of total predation only. PROC GENMOD in SAS, version 8.02 (Allison, 1999, SAS Institute, Cary, North Carolina) was used to run the analyses and

determine log-likelihood values, coefficient signs and p-values for each candidate model. Akaike's Information Criterion corrected for small sample size (AIC_c; Akaike, 1973; Burnham and Anderson, 2002; Mazerolle, 2004) was used to compare the models and single out the best candidate model (with the lowest AIC value) and set of variables. As suggested by in Burnham and Anderson (2002), $AIC < 2$ suggests substantial evidence for the model; values between 3 and 7 indicate that the model has considerably less support, whereas models with AIC values > 10 are very unlikely to explain the response variable.

Source-sink estimation

Viability of local populations established in the three landscape contexts was assessed using Pulliam's (1988) relationship expressed as $\lambda = P_a + P_j\beta$, where λ is the finite rate of increase at a site, P_a is the probability of adult female survival, P_j is the probability of female juvenile survival from fledging to the following breeding season, and β is the production of juvenile females per female per breeding season (annual fecundity). Local populations with a rate of increase inferior to one were considered sinks as opposed to sources for populations showing a rate of increase superior to one. Since we were unable to determine empirical probabilities for female adult and juvenile survival (P_a and P_j), we used estimates provided in the literature on Ovenbirds' demography (Roberts, 1971; Savidge and Davis, 1974; Greenberg, 1980; Temple and Cary, 1988; Gardalis et al., 2003; Grzybowski, 2005) to determine the minimum number of fledglings to be produced to maintain stable populations for a range of combinations of adult and juvenile annual survival rates.

To determine whether the sampled local populations were sources or sinks, we used Donovan et al., (1995) assumptions in calculating annual fecundity. First, we assumed that estimates of nesting success and nest failure (Mayfield, 1975) were constant throughout the breeding season. Second, we considered the average productivity per successful nest to be constant throughout the breeding season. Finally, we assumed that fecundity was constant regardless of breeding birds' age. Ovenbirds age can be determined by examining the wear pattern of the

third rectrix (Donovan and Stanley, 1995; Bayne and Hobson, 2002) with specimens in hand, but since we did not capture birds in this study, we could not subdivide fecundity per year by age (first-year vs. older breeders).

Results

Local habitat characteristics of woodlots breeding activity annual variation

Comparisons of vegetation variables measured in each sampled woodlots revealed similarities and differences in the composition and structure of forest stands (Table 2.2). First, canopy height, overall vegetation cover and tree basal area were similar among treatments indicating that our selection of study sites based on forest maps criteria (> 70 years old, > 17 m in height, > 60% density) was efficient in assessing these structural components. Significant differences were mainly between the continuous forest and woodlots in the agricultural matrix (regardless that they were isolated or connected). Litter depth, snag abundance, and percent cover of American beech (*Fagus grandifolia*) were significantly more developed in the continuous forest than in agricultural woodlots. Likewise, agricultural woodlots showed significantly more signs of forest management and human disturbances, with higher densities of small trees and higher percent cover of red maple (*Acer rubrum*) a tree species associated to disturbed sites (Brisson and Bouchard, 2003) (Table 2.2). All these differences indicated the fact that anthropogenic activities were more conspicuous in agricultural woodlots than in the continuous forest within the UNESCO Biosphere Reserve of Mont Saint-Hilaire.

Nesting success

Daily nest mortality was 0.122 in isolated woodlots, 0.063 in connected woodlots and 0.022 in the continuous forest (Chi-square, $df = 2$, $X^2 = 6.951$, $p < 0.05$; Table 2.4). Nesting success was considerably higher in the continuous forest than in isolated woodlots (Table 2.4). However, two-by-two treatment tests (Johnson, 1979, 1990) failed to show a significant difference between isolated and connected woodlots and between connected woodlots and the continuous forest. Mean number of female young per successful nest was 1.13 in isolated woodlots, 1.25 in connected woodlots and 2.17 in the continuous forest (Table 2.4). Consequently, fecundity per adult female per year was 0.11, 0.50 and 1.82 in isolated,

connected and continuous forests, respectively (Table 2.4). Within each of the three forest habitats, comparisons of nest success showed no significant differences between nesting periods (Table 2.5).

Predation, abandonment and parasitism

Daily mortality due to nest predation ranged from 0.022 in the continuous forest, to 0.052 in connected woodlots and to 0.098 in isolated woodlots (Chi-square, $df = 2$, $X^2 = 4.710$, $p < 0.10$; Table 2.4). Abandonment accounted for the remaining part of the nest failures and did not differ with respect to landscape context (Chi-square, $df = 2$, $X^2 = 2.358$, $p < 0.50$; Table 2.4). Parasitism was not observed in the continuous forest whereas 50% and 64.5% of the nests in connected and isolated woodlots were respectively parasitized (Table 2.4). While predation in most cases led to total nest failures, significant reduction in host Ovenbird young fledged due to partial predation and parasitism was also observed. Mean brood size of successful nests (i.e., nest where at least one Ovenbird young fledged) dropped from 3.9 to 2.8 fledged young where partial predation occurred (5 nests partially depredated over 17 nests; ANOVA, $F = 6.208$, $p = 0.025$; Figure 2.2). Also, mean brood size of successful nests (with at least one host young fledged) was reduced from 4.2 to 2.3 fledged birds in parasitized nests (7 parasitized nests over 17 successful nests; ANOVA, $F = 25.069$, $p < 0.001$; Figure 2.2).

Overall, only 1 nest out of the 24 monitored in the agricultural landscape was neither affected by brood parasitism, total predation nor partial predation. Nonetheless, that nest was abandoned. Out of the 8 nests having fledged at least one host juvenile in the agricultural landscape, the only one that was unparasitized was partially predated. On the other hand, none of the 11 nests monitored in the continuous forest were parasitized and one was partially preyed upon. Two nests were totally predated and did not complete their cycle.

Parasitism was associated with Brown-headed Cowbird abundance (Logistic fit, $n = 35$, $X^2 = 15.414$, $p < 0.001$, $R^2 = 0.327$) particularly in our isolated woodlots where these fragments

were visited twice as much by cowbirds than connected woodlots (Figure 2.3). However, there was no relationship between total predation and predator abundance (Logistic fit, $n = 35$, $X^2 = 0.089$, $p = 0.765$, $R^2 = 0.002$) and this trend was consistent between avian and mammalian predators (Figure 2.3). The combined effect of all predators and cowbirds was, however, significant among treatments where isolated fragments were more exposed, followed by connected woodlots and continuous forests (Table 2.6).

Environmental factors associated with predation and parasitism

Regression models of overall nest failure showed that an increase in the amount of cultivated fields surrounding woodlots and a reduction of local litter depth within these woodlots generated significantly lower breeding habitat quality. Akaike weights for these two models indicate that amount of agricultural land was a prevalent factor with more than 40.1% of the AIC weight (Table 2.7). Predation and parasitism effects on nest success of Ovenbirds were both highly linked with the importance of local forest management that came out as the best model and that carried 29.6% and 40.0% of the AIC weight for these causal factors. Cowbird parasitism was also positively associated with canopy openness within woodlots (28.9% of the AIC weight) and negatively associated with an increased amount of mature forest surrounding study sites within a 2 km radius (11.8% of the AIC weight); with AIC values under 2 for each of these models. Nest predation increased in woodlots with reduced litter depth (17.1% of AIC weight) surrounded by agricultural fields (13% of AIC weight). Overall, for the three response variables, local and landscape context variables came out as the best candidate models whereas woodlot size was less influential (Table 2.7).

Source-sink habitats

The number of fledglings required to maintain stable populations with regards to various combinations of estimates of juvenile and adult annual survival rates for Ovenbirds are presented in Table 2.8. Given our productivity results (Table 2.4) maintaining stable

populations in all forest habitats seems unlikely since it would require higher estimates than both the highest estimate for mean adult survival (0.845; Roberts, 1971) and highest estimate for juvenile survival (0.57; Grzybowski, 2005). On the other hand, the continuous forest is the only habitat that could maintain stable populations across the range of adult and juvenile survival rates (except when both survival rates reach their lowest values) (Table 2.4 and Table 2.8). Given that source and sink thresholds are generally based on averages for both adult and juvenile survival rates (Greenberg, 1980; Temple and Cary, 1988; Van Horn and Donovan, 1994; Donovan et al., 1995; Burke and Nol, 2000), the minimum number of fledglings that needs to be produced is 1.2 per adult female. At this source-sink threshold, Ovenbird local populations in fragmented woodlots (regardless of their isolation or connectedness) are considered sinks whereas the productivity of Ovenbird females in the continuous forest is high enough to maintain stable populations (Figure 2.4).

Discussion

Causal factors and nesting failures

In our study area, Ovenbirds nesting and fledgling success were significantly affected by forest fragmentation. Hence, as we predicted, ovenbirds were more successful in continuous forest and within fragmented woodlots, and were more successful in connected forests than in isolated fragments. Direct nest monitoring indicates that predation and parasitism strongly affected the nesting success of Ovenbirds in our fragmented forests. This corroborates results from other studies in highly fragmented landscapes where both predation and cowbird parasitism significantly affected breeding songbirds (Robinson et al., 1995a, 1995b; Donovan et al., 1997). In our study, predation rates in fragmented forests increased by a factor of 3 from continuous forests whereas predation was increased by a factor of 2 with regards to fragmented woodlots in south-central Ontario (Burke and Nol, 2000). Although our sample of monitored nests was too small to statistically show significant different predation rates between landscape contexts, nests within the fragmented landscape (isolated and connected woodlots) suffered a higher proportion of failure due to predation than nests in the large continuous forest. This difference in predation rates might be directly linked to predators abundance that seemed higher in the fragmented landscape³, which is a trend observed in several studies (Chalfoun et al., 2002b). For several predators, agricultural activities may also provide non-negligible food sources allowing them to concentrate within these habitats (Chalfoun et al., 2002b). Indeed, fragmentation induced by agriculture leads to a conversion of land uses that triggers a shift in the abundance and in the composition of the predator community with regards to continuous forest that may often increase the predation pressure on nesting songbirds (Morrell and Yahner, 1995; Oehler and Litvaitis, 1996; Bayne and Hobson, 1997; Heske et al., 2001, Chalfoun et al., 2002a). For instance, the release of meso-predator populations in agricultural landscapes is well documented and might represent the main factor

³ Although the predator abundance indicator showed no significant difference between treatments (Table 2.6).

behind forest birds' low reproductive success within these habitats (Schmidt, 2003). However, our study does not corroborate these general trends since occurrences of predators (birds and mammals) were not statistically different among forest treatments, although maximum abundance values were reached in isolated forests surrounded by agricultural fields.

Cowbird parasitism on Ovenbird's nests occurred in fragmented forests of the agricultural landscape but not in our study plots within continuous forest. This result is strongly correlated with high abundances of Brown-headed Cowbirds in our fragmented forests and low occurrences of cowbirds in the continuous forest. It also corroborates results obtained in other studies conducted in moderately to highly fragmented landscapes by agriculture (Brittingham and Temple, 1983; Lowther, 1993; Donovan et al., 1997; Morrison et al., 1999) where parasitism rates were high in both edge and core habitats of fragmented forests given the numerous feeding (agricultural fields) and nearby breeding (woodlands) habitats that such landscapes offer (Donovan et al., 1997). In our study area parasitism rates were two times more important in fragmented forests than forest fragments in south-central Ontario (Burke and Nol, 2000). Hence, even though brood parasitism effects were not as drastic as total nest failure due to predation, a significant reduction on brood size and number of fledglings has a direct effect on local recruitment of Ovenbirds in fragmented forests in our study area. This, in turn, had a direct influence on the local population rate of increase, which is influential in the source-sink population status of fragmented forests in the St. Lawrence valley.

Abandon rates were higher in fragmented forests of our study area than in south-central Ontario's fragmented forests (Burke and Nol, 2000). Such result may be correlated to higher partial brood loss following predation or brood parasitism that are thought to be factors driving nest abandonment (Van Horn and Donovan, 1994).

Factors associated with predation and parasitism

Donovan et al. (1997) showed that landscape-scale habitat patterns may influence nest predation and parasitism whereas Burke and Nol (2000) found that the amount of forest cover within a radius of 10 km had no effect on predation rates in woodlots but patch size had a major influence. In our study, we controlled for woodlot size by concentrating on woodlots with more than 23 ha of core area. Our regression models on overall nest failure, nest parasitism and nest predation show that both local and landscape scale factors are important in explaining the effects of predation and parasitism on Ovenbird nests. The composition of the matrix within which forest fragments are embedded came out as an important factor to explain the variation in nesting failures related to both predation and parasitism. The amount of agricultural fields within a radius of 2 km came out as our best model among the candidate models analysed to explain the variation in overall nest failure in our study sites and was ranked in third place to explain nest predation. Importance of predation effects in habitats adjacent to agricultural land may be explained, firstly, by an increased number of predators and a more diversified community of predators in agricultural landscapes (Bayne and Hobson, 1997; Kurki et al., 1998). Indeed, agricultural fields may also provide non-negligible food sources to many species allowing them to concentrate within these habitats (Chalfoun et al., 2002b). Its counterpart, the amount of mature forest, was also ranked in third place to explain nest parasitism that was less important when study sites were more surrounded by mature forest. Several studies have showed Brown-headed Cowbirds' preference for wood-field ecotones rather than extensive woods or prairie area (Gates and Gysel, 1978; Brittingham and Temple, 1983; Johnson and Temple, 1990; Lowther, 1993).

With regards to local factors, anthropogenic disturbances within woodlots (local forest management) had the most important positive influence on both nest predation and nest parasitism among the candidate models analysed. Finally, our results indicate that food quality indirectly measured through litter depth (Burke and Nol, 1998) might be important since it came out in second place in both overall nest failure and nest predation in our model selection

analyses. A similar study by Mattson and Niemi (2006) concluded that shallow leaf litter could exacerbate levels of nest failure and nest predation in habitats with low amounts of core forest where high abundances of inexperienced individuals (Holmes et al., 1996) and nest predators (Dijak and Thompson, 2000) are known to occur. Zarette et al., (2000) clearly showed that predation risk becomes higher in poor food quality environments where adults leave nest unattended for longer periods during feeding.

Productivity and Local population viability

In chapter 1, we found that ovenbird populations remained relatively constant over the two years of this study. Densities of territorial males and pairing success in woodlots (isolated and connected) of the agricultural matrix were similar to continuous forest. Whereas reproductive success assessed with a coarse-grain indicator such as presence of fledglings within male territories was significantly lower in the agricultural woodlots. Direct monitoring of nests further confirms that, in our study area, pairing success provides little insight into the effective value of woodlots for breeding productivity. This is contrary to Burke and Nol (2000) findings whereas ovenbirds' pairing success in fragmented forests of south-central Ontario was highly correlated with reproductive success. As observed in other studies conducted on forest birds in highly fragmented landscapes (Brawn and Robinson, 1996; Burke and Nol, 2000), Ovenbirds' local population dynamics and productivity were uncoupled in the St. Lawrence valley. Hence, assessment of habitat quality in fragmented forests for forest birds requires monitoring of reproductive success either from direct nest monitoring or from indirect approaches such as family groups focal surveys (chapter 1).

Our nesting data indicate that local populations established in fragments (isolated and connected woodlots) are likely to be sinks whereas populations in the four plots of the continuous forest can be considered sources. To be population sources, adult and juvenile annual survival in agricultural woodlots would have to be approximately 85% and 55% in connected forests and above these values in isolated forests. These survival rates are fairly

high and unlikely to occur on successive years (Van Horn and Donovan, 1994; Donovan et al., 1995). A higher sample of monitored nests is required to demonstrate with more statistical power the differences that were observed between our three forest habitats (continuous, isolated and connected fragments). Such monitoring should also be replicated on several years to measure the consistency over time of this important primary population parameter.

Despite the low reproductive success in our agricultural woodlots, the consistent patterns of occupancy and pairing success of Ovenbirds are indicative of a source-sink population dynamics where movement of birds from source populations to agricultural woodlots are likely. If so, consistent densities and pairing success over the years in farm woodlots may be linked to a stronger input of dispersing individuals from sources (Mont Saint-Hilaire or other continuous forest tracks) than individuals that reoccupy these woodlots after experiencing low reproductive success. Hence, dispersal of individuals in this system may, as in other highly fragmented landscapes, play a critical role in preventing regional population declines where productivity is low (Donovan et al., 1995; Brawn and Robinson, 1996; Burke and Nol, 2000). More research is thus needed on dispersal movements of individuals to better assess the demographic relationships between continuous forests and farm woodlots in fragmented landscapes such as those of the St. Lawrence valley. For instance, even though we have strong indications that Ovenbird populations in Mont Saint-Hilaire and the surrounding fragmented landscape are respectively population source and sinks, we do not know the scale at which such a dynamic occurs. Detailed information on natal dispersal of Ovenbirds across the fragmented landscape would be necessary to know whether Mont Saint-Hilaire source status is a direct benefit to its local sub-populations only or to the population at a larger scale. In a recent demographic study of adult survival through mark-recapture of Ovenbirds in fragmented and forested boreal landscapes, Bayne and Hobson (2002) found that lower nesting success and productivity in farm woodlots induced high turnovers in patch occupancy by individuals. They also observed a change in the age structure of breeders where a higher proportion of first-time breeders were found in fragments isolated by agriculture than in fragments created by timber harvesting or in continuous forest. Such pattern suggests that

higher nest failures in fragmented forests may drive a higher dispersal of breeders. Alternatively, first-time breeders in these fragmented forests could be more vulnerable to predation pressures and this in turn, could explain in part the lower fecundity in these forests. More in depth knowledge of local population's demography and age structure is needed to better understand the regional populations' dynamics of Ovenbirds in the St. Lawrence Lowlands landscape.

Conclusion

In our study all fragmented woodlots (isolated and connected) were large according to Burke and Nol (2000) criteria of large woodlots (> 23 ha in core area). The fecundity per adult female measured in these woodlots was, however, much lower than the one observed in large woodlots of southern Ontario (Burke and Nol, 2000). This result raises concerns on the vulnerability of regional populations of the Ovenbird in the St. Lawrence valley given that even large agricultural woodlots are sinks. It exacerbates the critical demographic role of continuous forest tracks such as the UNESCO Biosphere Reserve of Mont Saint-Hilaire that may be among the rare sites within the St. Lawrence valley where productivity exceeds mortality. Our results support the idea that preserving continuous tracks of forests is not only strategic in conservation planning but critical for preventing regional collapses of forest bird populations.

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Tables and figures

Figure 2.1 Map of the study area located in southern Québec, Canada.

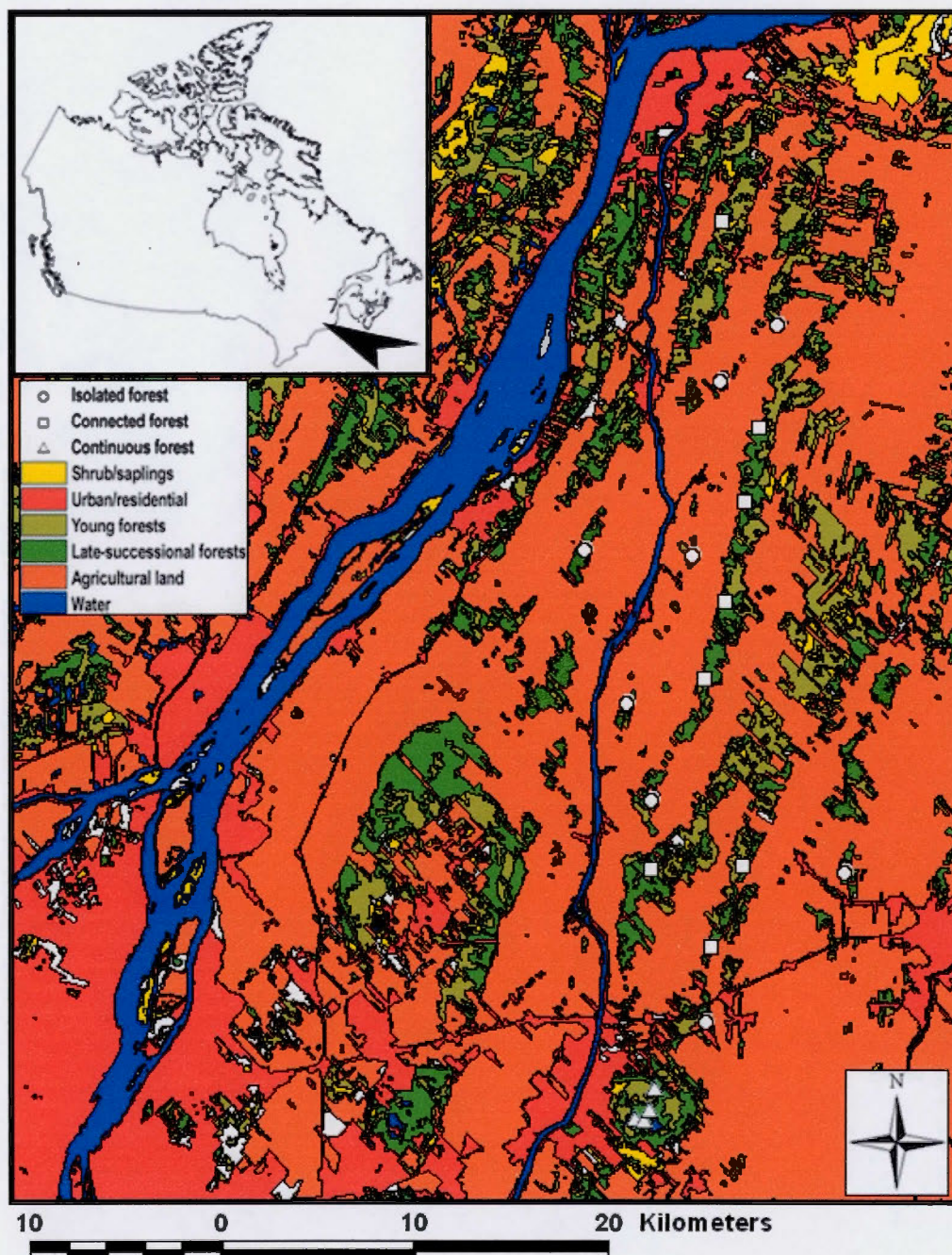


Table 2.1 Description of study sites in southern Québec, Canada.

<i>Study site</i>	<i>Habitat type</i>	<i>Distance to continuous forests¹</i>	<i>Agr. cover² (%)</i>	<i>Distance³ (m)</i>	<i>Total area⁴ (ha)</i>	<i>Core area⁵ (ha)</i>
11	Connected woodlot	Near	35.5	6352	1932.2	364.8
12	Connected woodlot	Near	73.4	6262	360.8	27.3
13	Isolated woodlot	Near	56.7	2688	174.7	73.9
24	Isolated woodlot	Near	80.1	6074	232.9	65.0
21	Connected woodlot	Near	74.0	8388	1004.6	612.0
22	Connected woodlot	Near	62.8	9356	260.2	136.6
23	Isolated woodlot	Near	85.6	7928	86.2	42.6
34	Isolated woodlot	Near	81.5	9526	209.2	114.8
31	Connected woodlot	Far	56.7	14741	1004.6	612.0
32	Connected woodlot	Far	54.2	18492	1295.1	854.4
33	Isolated woodlot	Far	86.2	14620	63.1	14.0
14	Isolated woodlot	Far	79.8	13067	81.1	40.9
41	Connected woodlot	Far	68.0	21605	1295.1	854.4
42	Connected woodlot	Far	47.4	28934	2345.2	665.6
43	Isolated woodlot	Far	76.8	26541	57.5	23.6
44	Isolated woodlot	Far	87.5	22358	44.3	15.1
M1	Continuous forest	-	0.4	-	1532.8	1051.2
M2	Continuous forest	-	1.8	-	1532.8	1051.2
M3	Continuous forest	-	3.6	-	1532.8	1051.2
M4	Continuous forest	-	12.4	-	1532.8	1051.2

¹ Near: <10 km from a continuous forest (>1000 ha core area) ; Far: > 10 km from a continuous forest.

² Proportion of agricultural cover within 2 km radius of sampling site.

³ Distance in meters from forest edge to a continuous forest (> 1000 ha core area).

⁴ Total area of forest patch.

⁵ Area of core forest patch containing study site, considering an edge buffer of 100 meters.

Table 2.2 Variation of local habitat characteristics (Mean \pm SE) between type of forest habitats (One-way ANOVA). Within 20 study sites, forest composition variables were calculated from data sampled from seven transects (60 m x 4 m) whereas other characteristics were measured at 21 vegetation-sampling points (isolated woodlots, n=8; connected woodlots, n=8; continuous forest, n=4).

	Isolated woodlots		Connected woodlots		Continuous forest		F (P)
	Mean	SE	Mean	SE	Mean	SE	
Forest composition							
<i>Acer saccharum</i> basal area (m ² /ha)	14.5	3.7	14.3	3.7	15.3	5.2	0.090 (0.914)
<i>Acer rubrum</i> basal area (m ² /ha)	12.6	2.0	14.0	2.0	0.5	2.8	8.464 (0.003)
<i>Fagus grandifolia</i> basal area (m ² /ha)	3.0	1.3	8.5	1.3	15.3	1.9	14.829 (<0.001) ³
<i>Tsuga canadensis</i> basal area (m ² /ha)	3.4	1.4	7.8	1.4	<0.1	1.9	5.920 (0.011)
Forest structure							
Tree basal area (m ² /ha)	45.2	3.1	50.7	3.1	37.8	4.4	2.946 (0.080)
Snag basal area (m ² /ha)	1.3	0.4	1.2	0.4	6.8	0.6	19.900 (<0.001)
Tree density, DBH 8-14cm (nb/ha)	424.9	42.1	328.1	42.1	247.0	59.5	3.464 (0.055)
Tree density, DBH 15-29cm (nb/ha)	452.4	33.9	410.7	33.9	244.0	47.9	6.498 (0.008)
Tree density, DBH >29cm (nb/ha)	200.1	19.7	242.6	19.7	181.5	27.9	1.966 (0.171)
Snag density, DBH 8-14cm (nb/ha)	35.7	7.5	25.3	7.5	11.9	10.6	1.716 (0.210)
Snag density, DBH 15-24cm (nb/ha)	15.6	3.9	11.2	3.9	34.2	5.5	6.127 (0.010)
Snag density, DBH >24cm (nb/ha)	6.0	3.7	4.5	3.7	52.1	5.2	18.096 (<0.001)
Mean DBH (cm)	20.6	0.9	22.5	0.9	22.9	1.2	1.722 (0.209)
Canopy height (m)	20.9	0.6	22.9	0.6	21.7	0.9	2.599 (0.104)
Sapling cover (2-10m; %)	30.2	1.8	29.9	1.8	41.4	2.6	7.641 (0.004)
Shrub cover (1-2m; %)	10.1	1.4	5.6	1.4	13.3	2.0	5.682 (0.013)
Vegetation cover (1m-canopy; %)	71.5	2.3	70.9	2.3	79.8	3.3	3.003 (0.076)
Ground cover (<1m; %)	39.1	4.7	36.1	4.7	22.4	6.6	2.101 (0.153)
Litter depth (mm)	85.8	3.6	88.7	3.6	145.8	5.1	38.498 (<0.001)
Perturbation indices							
Forest management ¹ (%)	50.9	2.7	51.2	2.7	0.6	3.9	55.670 (<0.001)
<i>Acer</i> management ² (%)	31.5	8.5	49.4	8.5	0.0	12.0	4.853 (0.022)

¹ Proportion of vegetation sampling points within study sites showing signs of logging activities.

² Proportion of vegetation sampling points within study sites showing signs of maple syrup production activities.

³ *Fagus grandifolia* basal area: Only local variable showing a significant difference between linear tracts and isolated woodlots (posthoc Tukey's HSD, $p = 0.024$).

Table 2.3 Description of variables used for generalized linear models.

<i>Variable</i>	<i>Description</i>
Local habitat	
Local vegetation cover	Mean proportion of vegetation cover (1m-canopy) (%)
Local ground cover	Mean proportion of ground covered with vegetation (%)
Local forest management	Human activity index ¹ (%)
Local litter depth	Mean litter depth (mm)
Landscape cover	
Patch core area	Area of core forest containing a study site (edge buffer: 100m; ha)
Agricultural cover	Proportion of agricultural land in a 2km radius (%)
Mature forest cover	Proportion of mature forest in a 2km radius (%)
Distance to continuous forests	Distance to closest forest of >1000 ha in core area (m)

¹ Calculated from logging presence/absence at each vegetation sampling point within study sites.

Table 2.4 Reproductive success of Ovenbird in isolated woodlots, connected woodlots and a continuous forest in southern Québec.

Habitat	n ¹	Obs. Days ²	Daily mortality	Daily survival	Daily survival SE	Nest success	Cause-specific daily mortality ³	Abandonment	Apparent parasitism rate ⁴	Female fledglings per successful nest	Fecundity per adult female per year ⁵
Isolated woodlots	14	82	0.122	0.878	0.036	0.050	0.098	0.024	0.643	1.13	0.11
Connected woodlots	10	96	0.063	0.938	0.024	0.227	0.052	0.010	0.500	1.25	0.50
Continuous forest	11	91	0.022	0.978	0.015	0.600	0.022	0	0	2.17	1.82
X ² , df			6.951, 2				4.710, 2	2.358, 2			
(P)			(<0.05)				(<0.10)	(<0.50)			

¹ n = total nest sample size.² Obs. days = the total number of observation days pooled across all nests within each habitat type.³ Daily mortality is partitioned by cause of failure.⁴ Apparent parasitism rate = total number of parasitized nest divided by total number of nests.⁵ Fecundity per adult female per year = the mean number of female offspring successfully fledged per adult female per year.**Table 2.5** Incubation and brooding success of Ovenbird in isolated woodlots, connected woodlots and a continuous forest in southern Québec.

Habitat	n	Obs. days	Laying – incubation (15 days)			Obs. days	Brooding (8 days)			Nest Success	X ² , df (P)
			Daily mortality	Daily survival	Daily survival SE		Daily mortality	Daily survival	Daily survival SE		
Isolated woodlots	14	52	0.096	0.904	0.041	0.219	0.167	0.833	0.068	0.233	0.883, 1 (<0.50)
Connected woodlots	10	57	0.053	0.947	0.030	0.444	0.077	0.923	0.043	0.527	0.233, 1 (<0.70)
Continuous forest	11	39	0	1	0	1	0.038	0.962	0.027	0.731	1.534, 1 (<0.30)
X ² , df			4.029, 2				4.155, 2				
(P)			(<0.20)				(<0.20)				

Figure 2.2 Effect of a) partial predation on brood size of nests having fledged at least one Ovenbird ($n=17$, $F=6.208$, $p=0.025$) and b) brood parasitism on brood size of nests having fledged at least one Ovenbird young ($n=17$, $F=25.069$, $p<0.001$). Boxes represent mean \pm SE; vertical lines represent 95% confidence intervals.

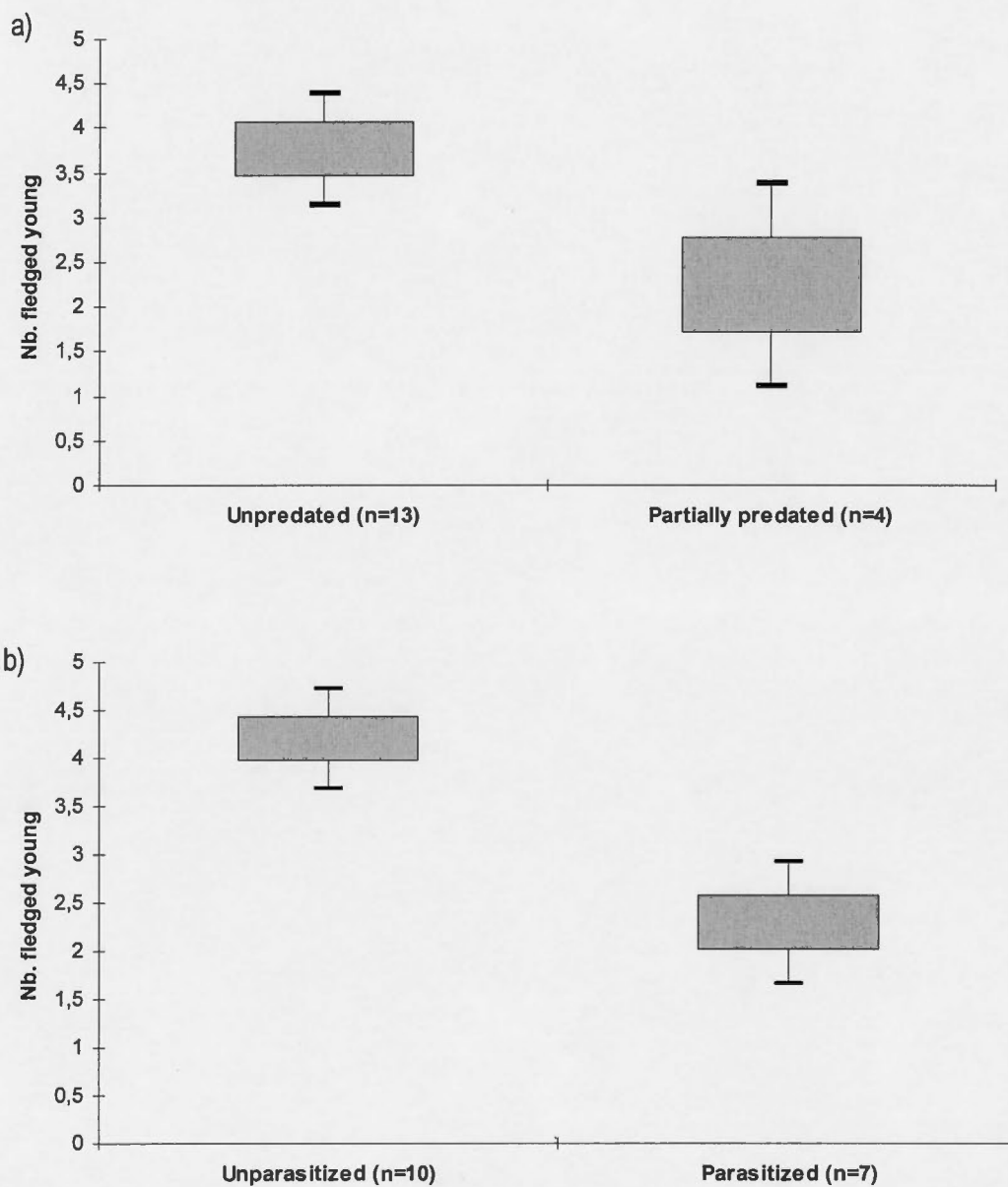


Figure 2.3 Relationship between a) brood parasitism and Brown-headed Cowbird mean abundance ($n=35$, $X^2=15.414$, $p<0.001$, $R^2=0.327$) and b) total predation and mean abundance of predators ($n=35$, $X^2=0.089$, $p=0.765$, $R^2=0.002$).

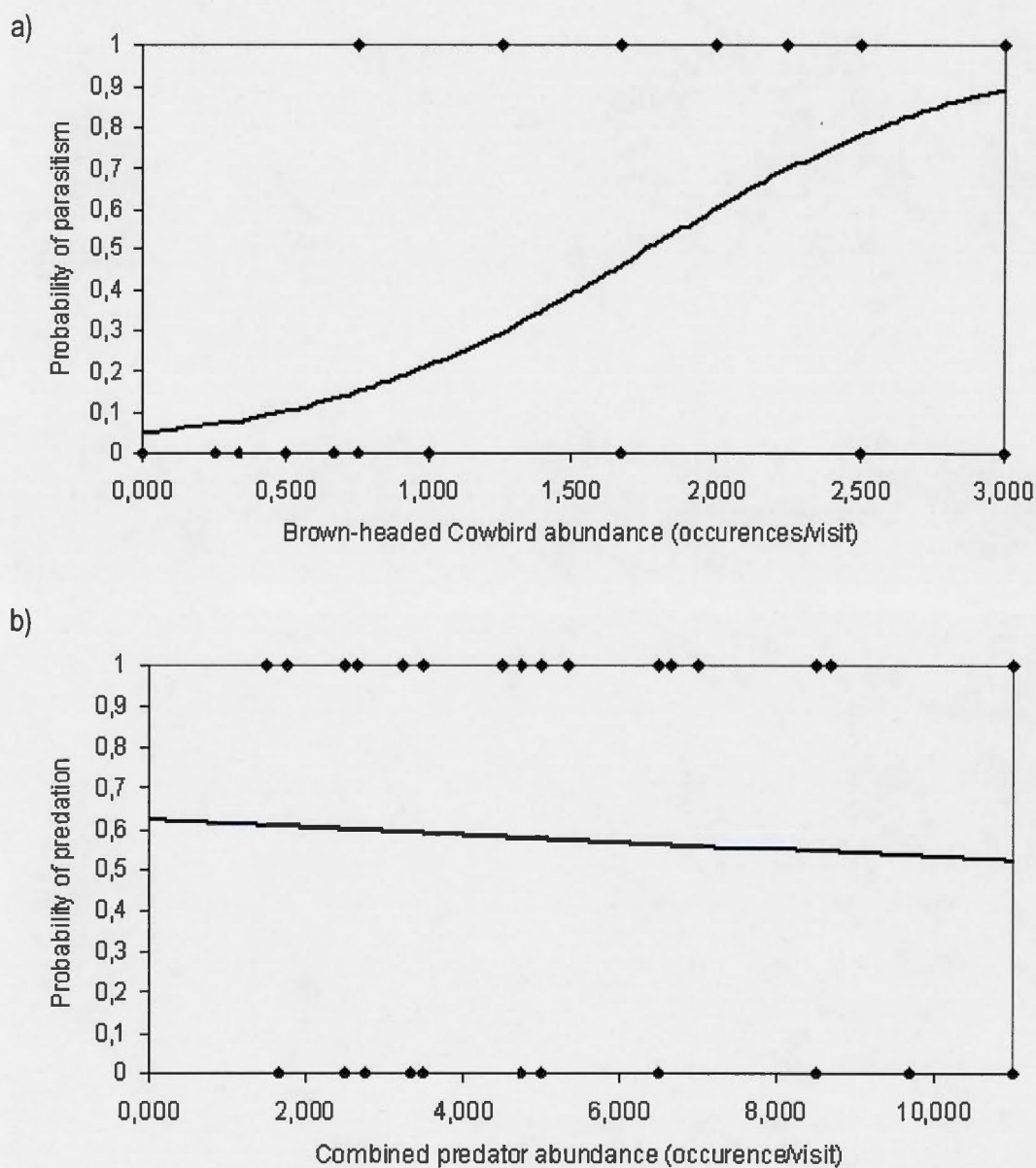


Table 2.6 Mean abundance measured as number of occurrences per visit to sampling sites for Brown-headed Cowbird, avian predators and mammalian predators.

	<i>Brown-headed Cowbird (occ./visit)</i>	<i>Avian predators (occ./visit)</i>	<i>Mammalian predators (occ./visit)</i>	<i>Avian and mammalian predators (occ./visit)</i>	<i>Combined abundance (occ./visit)¹</i>
Isolated woodlots (n=16)	2.08	1.55	1.90	3.45	5.53
Connected woodlots (n=16)	0.95	1.67	1.52	3.19	4.14
Continuous forest (n=8)	0.30	1.09	1.70	2.79	3.09
F statistic	17.254	0.791	0.284	0.231	3.329
(P value)	(<0.001)	(0.461)	(0.754)	(0.795)	(0.047)

¹ Combined mean abundance includes all categories of predators and Brown-headed Cowbird.

Table 2.7 Logistic regression models for Ovenbird nesting failure, brood parasitism and total predation.

<i>Model</i>	<i>Coefficient sign (P value)</i>	<i>K¹</i>	<i>LL²</i>	<i>AICc³</i>	<i>Δ AIC⁴</i>	<i>AICc Weight⁵</i>
<i>Nest failure</i>						
1. Agricultural cover	+ (0.010)	2	-20.2468	45.494	0	0.401
2. Local litter depth	-(0.021)	2	-21.0592	47.118	1.625	0.178
3. Patch core area	-(0.027)	2	-21.4571	47.914	2.421	0.120
4. Local forest management	+(0.030)	2	-21.5474	48.095	2.601	0.109
5. Mature forest cover	-(0.046)	2	-21.9877	48.975	3.482	0.070
6. Local ground cover	-(0.069)	2	-22.4152	49.830	4.337	0.046
7. Local vegetation cover	-(0.174)	2	-24.2459	50.799	5.306	0.028
8. Null	-	1	-22.9600	50.920	5.426	0.027
9. Distance to continuous forests	+(0.122)	2	-23.2679	51.536	6.042	0.020
10.Global	-	9	-8.9102	71.820	26.327	<0.001
<i>Nest parasitism</i>						
1. Local forest management	+(0.015)	2	-17.0864	39.173	0	0.296
2. Local vegetation cover	-(0.008)	2	-17.1104	39.221	0.048	0.289
3. Mature forest cover	-(0.010)	2	-18.0057	41.011	1.839	0.118
4. Agricultural cover	+(0.007)	2	-18.1680	41.336	2.163	0.100
5. Local litter depth	-(0.017)	2	-18.2508	41.502	2.329	0.092
6. Local ground cover	-(0.011)	2	-18.2710	41.542	2.369	0.090
7. Distance to continuous forests	+(0.019)	2	-20.3157	45.631	6.459	0.012
8. Null	-	1	-23.5554	49.418	10.246	0.002
9. Patch core area	-(0.119)	2	-22.2903	49.581	10.408	0.002
10.Global	-	9	-12.7353	79.471	40.298	<0.001
<i>Nest predation</i>						
1. Local forest management	+(0.010)	2	-20.1525	45.305	0	0.400
2. Local litter depth	-(0.020)	2	-21.0037	47.007	1.702	0.171
3. Agricultural cover	+(0.023)	2	-21.2778	47.556	2.251	0.130
4. Patch core area	-(0.042)	2	-21.8864	48.773	3.468	0.071
5. Local ground cover	-(0.050)	2	-21.9725	48.945	3.640	0.065
6. Local vegetation cover	-(0.067)	2	-22.2825	49.565	4.260	0.047
7. Mature forest cover	-(0.068)	2	-22.2998	49.600	4.295	0.047
8. Distance to continuous forests	+(0.091)	2	-22.4087	49.817	4.512	0.042
9. Null	-	1	-24.1314	50.570	5.265	0.029
10.Global	-	9	-11.1596	76.319	31.014	<0.001

¹ Number of parameters including the intercept.² Maximised log-likelihood³ Akaike's Information Criterion corrected for small sample size.⁴ Increase in AICc over the lowest observed value of AICc.⁵ Akaike weight, strength of evidence that the model is best of the set.

Figure 2.4 Comparison of juvenile production (\pm SE) by female Ovenbirds in isolated woodlots, connected woodlots and continuous forest in southern Québec, Canada. The solid line indicates the threshold for source-sink habitat designation ($\beta = (\lambda - P_a) / P_j$; Adult annual mortality (P_a): 0.623, Juvenile annual mortality (P_j): 0.31, Rate of increase (λ): 1.0, Productivity threshold (β): 1.22).

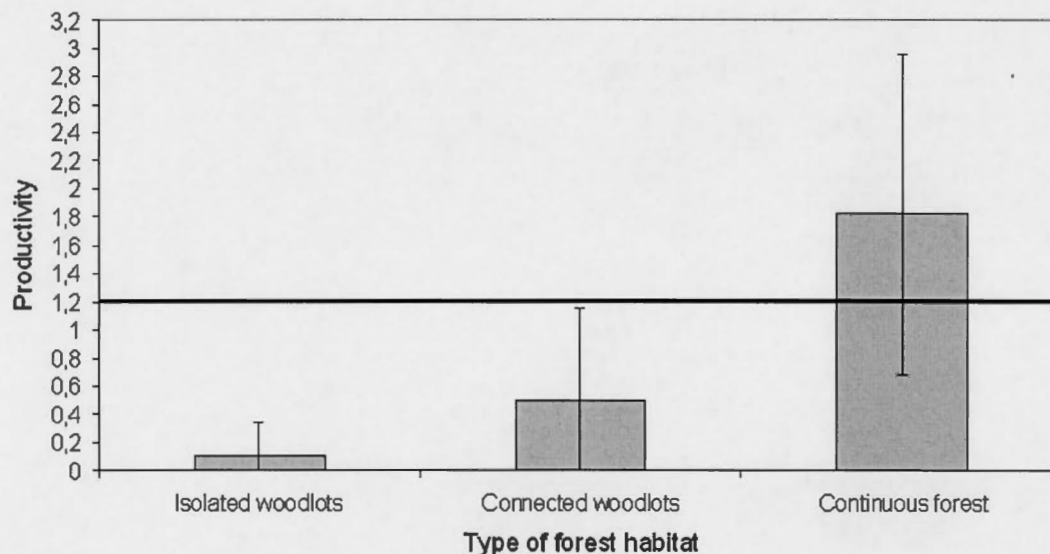


Table 2.8 Ovenbird productivity thresholds (production of female juveniles per adult female) for determining source-sink population status given specific juvenile and adult survival rates.

Juvenile annual survival	Adult annual survival		
	Lowest (0.540) ¹	Mid (0.623) ²	Highest (0.845) ³
Low (0.25) ⁴	1.84	1.51	0.62
Mid (0.31) ²	1.48	1.22	0.50
High (0.57) ⁵	0.81	0.66	0.27

¹ Savidge and Davis 1974

² Average of the published adult survival estimates (Burke and Nol 2000; Donovan et al., 1995)

³ Roberts 1971

⁴ Gardali et al., 2003

⁵ Grzybowski 2005

CONCLUSION GÉNÉRALE

Les modifications apportées à l'habitat de reproduction de la faune aviaire forestière peuvent d'abord se traduire par une réduction de l'abondance et du succès d'appariement de ces espèces (Villard et al., 1993; Van Horn et al., 1995). De plus, certains auteurs (Vickery et al., 1992; Zarette, 2001) montrent que malgré des indices d'abondance et de succès d'appariement élevés, ces derniers n'assurent pas le niveau de succès reproducteur nécessaire au maintien des populations locales. Nos résultats pointent dans cette direction alors que l'abondance et le succès d'appariement de la Paruline couronnée sont comparables entre les forêts fragmentées (isolées et connectées) et les sites d'étude de la forêt continue, mais le succès reproducteur est de façon statistiquement significative inférieur dans les forêts fragmentées. L'activité reproductrice de la Paruline couronnée dans cette région du Québec dépend donc grandement de facteurs qui affectent les étapes de l'incubation et du nourrissage des jeunes, plutôt que des mécanismes de dispersion et de sélection du site de nidification par les individus adultes. Nos résultats indiquent clairement la présence d'effets dus à la fragmentation du couvert forestier sur la productivité en juvéniles.

2.1 Faible variabilité inter-annuelle

La faible variabilité inter-annuelle des résultats obtenus au cours des deux années de l'étude est indicatrice d'une certaine stabilité dans la dynamique des populations de Paruline couronnée sur notre territoire. Nos estimations des paramètres démographiques (densité des mâles territoriaux, succès d'appariement et succès de reproduction) sont similaires pour les années 2004 et 2005, notamment le succès de reproduction qui a montré des valeurs significativement inférieures dans les habitats isolés durant les deux saisons de nidification. L'abondance et le succès d'appariement sont demeurés élevés peu importe le contexte d'isolement.

L'abondance des mâles territoriaux et le taux d'appariement élevés et semblables entre nos deux années de travaux dans les habitats isolés indiquent que les faibles succès de reproduction de la première année n'affectent ni le nombre de mâles territoriaux qui s'installent dans ces bois à la deuxième année ni l'abondance des femelles qui s'apparient aux mâles. Ce résultat est suggestif du rôle de la forêt continue comme habitat source dans une dynamique de population source-puits (Pulliam et al., 1988). Dans ce système, le recrutement d'individus en dispersion doit forcément être un facteur important à sa stabilité démographique.

2.2 Forêts isolées et forêts continues

Les oiseaux nicheurs sont habituellement peu fidèles aux aires de reproduction de faible qualité. Plusieurs études ayant suivi la nidification d'espèces affectées par la fragmentation ont publié des résultats montrant de très faibles taux de retour aux sites ayant produit peu de juvéniles ou ayant connu un taux d'échec élevé l'année précédente (Roth et Johnson, 1993; Haas, 1998; Pomeluzi and Faaborg, 1999; Bayne and Hobson, 2002; Pomeluzi, 2003). Il apparaît donc raisonnable de présumer qu'une abondance élevée et récurrente dans les milieux peu productifs est directement liée au recrutement d'individus se dispersant à partir d'habitats sources.

Ces résultats sont en accord avec la théorie des métapopulations (Hanski, 1991). Cette dernière confère une grande importance aux mouvements des individus entre les populations locales. Ces mouvements réduisent les probabilités d'extinction locale et accentuent les chances de colonisation de nouveaux habitats (Hanski et Gilpin, 1997). En montrant que des habitats de reproduction de faible qualité (peu productifs) sont occupés sur une base régulière, nos résultats suggèrent un phénomène de forts déplacements entre les populations locales.

Une réduction de l'immigration provenant des populations sources environnantes et/ou l'accentuation de la fragmentation des habitats forestiers rémanents pourraient induire une

diminution de l'abondance des espèces aviaires et nuire à l'appariement dans les habitats isolés. Ceci aurait des répercussions directes sur un succès reproducteur déjà faible et réduirait davantage la viabilité de ces populations. Ces conditions pourraient causer d'importantes réductions du succès de reproduction à l'échelle du paysage et rendre les populations occupant les habitats forestiers isolés encore plus dépendantes de la production de juvéniles des grandes forêts continues.

Les forêts continues sont plus favorables à la reproduction des oiseaux forestiers que les forêts isolées où de faibles proportions du couvert forestier sont complètement enclavées par la matrice agricole. En raison de la faible contribution en apport de juvéniles de ces habitats isolés, le recrutement d'individus et la stabilité des populations locales dépendent de la production des populations sources environnantes et de la capacité de ces nouveaux individus à se disperser dans le paysage fragmenté. Nous estimons donc que la viabilité à long terme des populations occupant les habitats forestiers isolés sur notre aire d'étude est fortement liée à la production de juvéniles des forêts continues.

2.3 Causes d'échecs de la nidification

Les insuccès de la nidification dans les habitats isolés par l'agriculture sont généralement attribués à la prédation et au parasitisme par le Vacher à tête brune (Brittingham et Temple, 1983; Wilcove, 1985; Lowther, 1993; Donovan et al., 1995; Porneluzi et Faaborg, 1999; Burke et Nol, 2000; Heske et al., 2001; Chalfoun et al., 2002b). L'importance des effets de la prédation et du parasitisme peut d'abord être expliquée par la richesse élevée en espèces, autant proies que prédateurs, retrouvée dans ces milieux. Cette richesse serait tributaire de la diversité des habitats et des sources non-négligeables de nourriture introduites au système par les activités agricoles qui encouragent plusieurs espèces à se concentrer à l'interface des forêts et des champs agricoles (Chalfoun et al., 2002b). Cette hausse de la concentration des

proies potentielles en lisières se traduit par l'augmentation de l'occurrence des prédateurs à ces endroits spécifiques.

Conséquemment, la fragmentation peut, par l'insertion de nouveaux éléments d'habitats dans un paysage naturel, déclencher ou accentuer des changements au sein de la communauté de prédateurs (Bayne and Hobson, 1997; Heske et al., 2001; Chalfoun et al., 2002a). Ainsi, l'effet de la prédation gagne en intensité dans les milieux perturbés parce que les espèces locales de forêts profondes sont potentiellement moins adaptées à cette abondance inhabituelle de prédateurs aviaires et mammaliens qui bénéficient des habitats transformés par l'activité humaine. Par exemple, le relâchement des populations de meso-prédateurs dans les paysages agricoles est bien documenté et reconnu comme étant l'un des principaux facteurs expliquant la réduction du succès de la nidification dans ces milieux (Schmidt, 2003). Les hauts taux de prédation que nous avons observés dans les habitats isolés sont en lien avec cette hypothèse.

De plus, les taux élevés de parasitisme par le Vacher à tête brune observés dans le paysage fragmenté, phénomène qui était absent de la forêt continue, indiquent que la dynamique de ce processus s'apparente grandement à celle de la prédation. L'effet du parasitisme est plus important dans les milieux associés à l'activité humaine qu'en forêt profonde. Cette tendance, rapportée dans de nombreuses études (Brittingham and Temple, 1983; Lowther, 1993), semble être principalement associée à l'abondance du Vacher à tête brune dans les milieux perturbés par l'agriculture.

Bien que les effets du parasitisme et de la prédation partielle n'aient pas été aussi drastiques que celui de la prédation totale⁴, ces processus ont significativement influencé la taille des couvées et la production de juvéniles. Ce dernier paramètre influence directement le taux de

⁴ De notre échantillon de nids de Paruline couronnée, plusieurs nids parasités et/ou ayant partiellement subi de la prédation ont mené des juvéniles hôtes à l'envol.

croissance des populations locales qui est un facteur à la base du statut source-puit que peut prendre une population biologique.

2.4 Projets futurs

La stabilité des paramètres démographiques de cette étude, notamment le succès élevé de reproduction tant mesuré par notre indicateur (présence d'un jeune dans un territoire de couple nicheur, chapitre 1) que par le suivi direct de nids (chapitre 2), suggèrent que le Mont Saint-Hilaire est un environnement forestier clé dans le maintien de la population régionale de Paruline couronnée dans le secteur de la vallée du Saint-Laurent que nous avons étudié.

Nos résultats indiquent que la population de Paruline couronnée du Mont Saint-Hilaire produit un nombre de jeunes qui est au-delà du niveau requis pour le maintien de la population à l'échelle locale tandis que les forêts du paysage agricole fragmenté (isolés et connectées) produisent un nombre insuffisant de jeunes pour se maintenir. L'apparente stabilité dans l'abondance et le taux d'appariement de la Paruline couronnée dans les bois agricoles repose donc sur un apport extérieur et non sur leur capacité intrinsèque de renouvellement. Cette fragilité du statut démographique de la Paruline couronnée en plaine agricole est d'autant plus préoccupante que notre étude n'a ciblé que des bois suffisamment grands (c'est-à-dire, des bois avec plus de 23 ha de forêt profonde ; ceux-ci ne représentent que 10,5% des bois de la région mais comprennent 92,9% de la matrice de forêt profonde régionale) pour offrir des conditions adéquates à cette espèce, sachant à l'avance que les plus petits bois montrent une productivité encore plus faible (Burke and Nol, 2000). La dynamique de population à l'échelle régionale semble donc reposer fortement sur le maintien de massifs tels que celui du Mont Saint-Hilaire.

Des études de suivis directs sur les nids (Burke et Nol, 2000; Bourque et Villard, 2001) telles que celle que nous avons menée au chapitre 2, mais sur de plus grands effectifs et pour une plus longue durée (plusieurs années) sont nécessaires pour clairement mesurer l'influence

relative de la communauté de prédateurs, du parasitisme des couvées et de la qualité de l'habitat (notamment en regard des ressources alimentaires) (Burke et Nol, 1998; Zanette et al., 2000) sur les activités de nidification et les échecs de la reproduction à une plus grande échelle sur le territoire de la vallée du Saint-Laurent. Cette information préciserait davantage le potentiel des grandes forêts régionales à assurer le maintien des populations d'oiseaux forestiers des Basses-terres du Saint-Laurent. Pour le moment, nous savons que les grandes forêts sont de meilleurs habitats de reproduction et produisent plus de juvéniles que les forêts fragmentées. Mais en produisent-elles suffisamment pour le maintien à long terme des populations régionales? Des efforts de recherche doivent être faits en ce sens.

Pour cerner le rôle du Mont Saint-Hilaire comme habitat source et mesurer sa portée spatio-temporelle dans la dynamique régionale des populations d'oiseaux nicheurs, il s'avèrera également nécessaire de mieux comprendre la dispersion des individus à l'échelle du paysage. La méthode CMR (capture-marquage-recapture) et les suivis télémétriques pourraient être utilisés afin d'examiner avec précision les relations démographiques entre les forêts continues et les forêts isolées, notamment le Mont Saint-Hilaire et les forêts avoisinantes. Enfin, en fondant nos stratégies de conservation des forêts du Sud du Québec (corridors forestiers, liens entre les habitats forestiers de la plaine agricole et massifs) sur ces connaissances nous augmentons les chances de maintien à long terme de l'avifaune forestière dans des territoires fortement aménagés (Bennett, 1999) tels que ceux de la vallée du Saint-Laurent.

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APPENDICE A

ACTIVITÉS REPRODUCTRICES DE TROIS AUTRES ESPÈCES SENSIBLES AUX CONDITIONS D'INTÉRIEUR DE FORÊT

Voici les données recueillies lors de la première collecte de données (été 2004) auprès des populations de Grive des bois (*Hylocichla mustelina*), de Tangara écarlate (*Piranga olivacea*) et de Paruline bleue (*Dendroica caerulescens*). Les données concernant ces trois espèces n'ont pas été prises en considération lors des analyses en raison de la faible taille de l'échantillon (en 2004, 44 territoires pour ces trois espèces combinées comparativement à 112 pour la Paruline couronnée). L'effort d'échantillonnage de la deuxième collecte de données a particulièrement été axé sur la nidification de la Paruline couronnée.

Tableau A.1 Abondance, taux d'appariement et succès de reproduction de la Paruline bleue, la Grive des bois et le Tangara écarlate en 2004, sur notre aire d'étude, Québec, Canada.

	Densité des mâles territoriaux (nb/ha)	Taux d'appariement (/1)	Succès de reproduction (/1)
<i>Paruline bleue</i>			
Forêt continue (n=6)	0,133	1,000	0,500
Forêts connectées (n=8)	0,089	0,750	0,125
Forêts isolées (n=0)	0	-	-
Forêts adjacentes ¹ (n=3)	0,033	1,000	0,000
Forêts éloignées ² (n=5)	0,056	0,600	0,200
<i>Grive des bois</i>			
Forêt continue (n=5)	0,111	0,400	0,400
Forêts connectées (n=4)	0,044	0,500	0,000
Forêts isolées (n=7)	0,078	0,571	0,429
Forêts adjacentes (n=8)	0,089	0,625	0,250
Forêts éloignées (n=3)	0,033	0,333	0,333
<i>Tangara écarlate</i>			
Forêt continue (n=2)	0,044	0,500	0,000
Forêts connectées (n=7)	0,078	0,571	0,000
Forêts isolées (n=5)	0,056	0,800	0,200
Forêts adjacentes (n=3)	0,033	0,667	0,000
Forêts éloignées (n=9)	0,100	0,667	0,111

¹ Combine les forêts connectées et isolées qui sont situées à < 10 km d'une forêt continue (>1000 ha de forêt profonde).

² Combine les forêts connectées et isolées qui sont situées à > 10 km d'une forêt continue (>1000 ha de forêt profonde).